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A Theory for Cyclic Shifts between Alternative States in Shallow Lakes

Egbert H. van Nes,[1,*] Winnie J. Rip,[2] and Marten Scheffer[1]

[1]*Aquatic Ecology and Water Quality Management Group, Wageningen University and Research Center, P.O. Box 8080, NL-6700 DD Wageningen, The Netherlands;* [2]*Waterboard Amstel, Gooi & Vecht. P.O. Box 1061, NL-1200BB Hilversum, The Netherlands*

Abstract

Some shallow lakes switch repeatedly back and forth between a vegetation dominated clear-water state and a contrasting turbid state. Usually such alternations occur quite irregularly, but in some cases the switches between states are remarkably regular. Here we use data from a well-studied Dutch lake and a set of simple models to explore possible explanations for such cyclic behavior. We first demonstrate from a graphical model that cycles may in theory occur if submerged macrophytes promote water clarity in the short run, but simultaneously cause an increased nutrient retention, implying an accumulation of nutrients in the long run. Thus, although submerged plants create a positive feedback on their own growth by clearing the water, they may in the long run undermine their position by creating a slow ''internal eutrophication''. We explore the potential role of two different mechanisms that may play a role in this internal eutrophication process using simulation models: (1) reduction of the P concentration in the water column by macrophytes, leading to less outflow of P, and hence to a higher phosphorus accumulation in the lake sediments and (2) a build-up of organic matter over time resulting in an increased sediment oxygen demand causing anaerobic conditions that boost P release from the sediment. Although the models showed that both mechanisms can produce cyclic behavior, the period of the cycles caused by the build-up of organic material seemed more realistic compared to data of the Dutch Lake Botshol in which regular cycles with a period of approximately 7 years have been observed over the past 17 years.

Key words: slow–fast cycles; *Chara* sp.; singular perturbation approach; infinite-period bifurcation; alternative stable states; internal eutrophication.

Introduction

Shallow lakes are among the best studied examples of ecosystems with alternative stable states (Scheffer and others 2001). Most of these lakes are either rather turbid and devoid of submerged macrophytes or clear and vegetated (Scheffer and others 1993). Excessive nutrient loading has caused most lakes in populated areas to shift to the turbid state. Upon reduction of the nutrient loading lakes may shift back to the clear state, but the critical nutrient level at which the shift back occurs is typically lower than the nutrient level at which the ecosystem switched to the turbid state. Lakes that do not clear up upon reduction in the nutrient load can sometimes be forced to the clear state by taking out most of the fish (Shapiro and Wright 1984; Meijer and others 1999). Such biomanipulation can leave the lake permanently clear if the nutrient level is low enough to allow the alternative clear state to be stable. Natural events such as alterations in the water level, heavy storms, or natural fish kills may also cause a shift between the alternative stable states (Scheffer 1998).

In some lakes repeated shifts between a clear and a turbid state have been observed. Examples include the Swedish Lake Tåkern and Lake

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*Corresponding author; e-mail: egbert.vannes@wur.nl

Krankesjön (Blindow 1992; Blindow and others 1993, 2002). Tomahawk Lagoon in New Zealand (Mitchell 1989), the English Alderfen Broad (Perrow and others 1994) and flood plain lakes in the Netherlands (Van Geest and others 2006, this volume). Such shifts occur irregularly in most lakes, suggesting that they are the result of some stochastic external forcing, such as fluctuations in the water level or changes in phosphorus load. However, in some lakes remarkably regular oscillations between alternative states have been observed. The best documented examples that we are aware of are the English lake Alderfen Broad (Figure 1) (Moss and others 1990; Perrow and others 1994) and the Dutch Lake Botshol (Figure 2) (Simons and others 1994; Rip and others 2005). Both lakes have a cyclic dominance of macrophytes with a period of approximately 7 years. One explanation of such behavior may be that there is a regular external forcing on the system (Ouboter and Rip 2006). However, an alternative possibility is that there is an intrinsic process that causes regular cycles. We first describe the patterns found in Lake Botshol. Subsequently, we show graphically what the theoretical prerequisites for cycles in shallow lakes are, according to ''slow–fast theory'' (Muratori and Rinaldi 1991; Rinaldi and Scheffer 2000). Finally, we propose two candidate mechanisms and use simple models to analyze whether these mechanisms could theoretically generate regular cycles with realistic periods. We compare the model results with field data of Lake Botshol.

Cyclic Behavior of Lake Botshol

A detailed description of Lake Botshol (287 ha, mean depth 3 m) is given by Rip and others (2005). From 1985 on, mapping of submersed macrophytes has been performed each summer, except for the year 1986. In period 1985–2000 and 2003 a transect pattern covering most of the open water and pools, watercourses and ditches have been followed each time. The plant material was observed and collected by dredging and snorkeling. Dredging has been done with a special apparatus developed and described by Satake (1987). Total P, chlorophyll-a and Secchi-disc depth were determined according to the international standards (ISO). During different periods, samples were taken daily, at two-weekly intervals, or four times per year.

The Botshol ecosystem showed oscillations in total phosphorus and vegetation coverage during the 17-year study period (Figure 2A). Along with these oscillations, the water clarity and the chlorophyll-a concentration showed regular cycles (Rip and others 2005). The period of the cycles of all relevant variables was approximately 7 years. The approximate range for alternative stable states can be shown by plotting macrophyte coverage versus total phosphorus (Figure 2B). Apart from an unexplained increase of total P between 1998 and 2001, the cycles suggest two critical *P* values: one for shifting to a vegetation dominated state at approximately 0.02 mg L^{-1} and one for loss of vegetation at 0.04 mg L^{-1}.

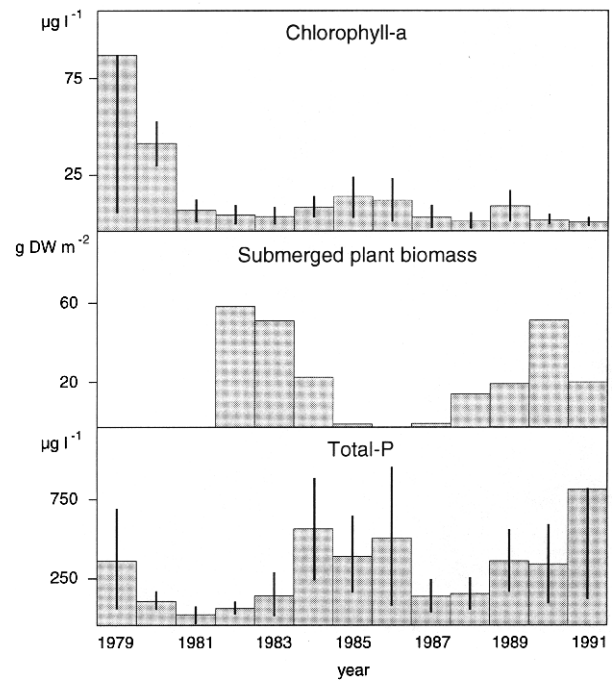

Figure 1. Changes in the mean summer concentrations of chlorophyll-a and total P and in the biomass of submerged plants in Alderfen Broad, UK, following disconnection of the lake from a nutrient rich inflow stream. Redrawn from Perrow and others (1994).

A Graphical Analysis of Intrinsic Cycling

In our search for mechanisms that might cause cyclic shifts in lakes, we will first explore a graphical theory of how a system with alternative equilibria could become cyclic. This geometric analysis of the slow–fast system is known as the singular perturbation approach (see overview by Rinaldi and Scheffer 2000).

We start with a model of a shallow lake with alternative states, that is slightly different from the classical one (Scheffer and others 1993), in which nutrients were considered as a fixed parameter. In reality the nutrient content of a lake is a slow

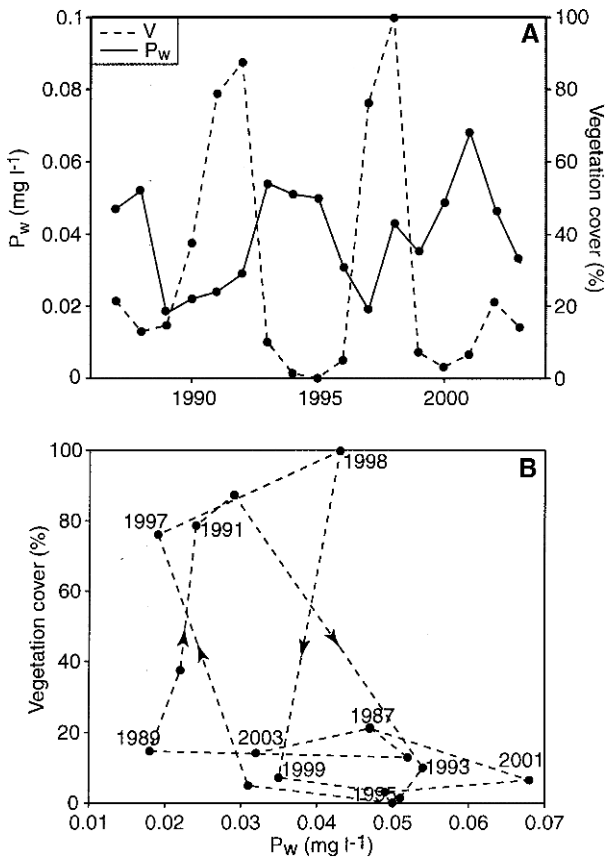

Figure 2. (**A**) Summer averages of vegetation cover and total P at Grote Wije in Botshol during 1987–2003 (Rip and others 2005). (**B**) Observed cycles in Botshol.

variable driven by differences between nutrient loading and losses. Therefore the limiting nutrient concentration should actually be considered as a dynamical state variable instead of a parameter. In our model, we assume that the equilibrium biomass of vegetation plotted against the nutrient level has a ''catastrophe fold'' implying that for a range of nutrient levels there are two stable vegetation densities separated by an unstable (dotted) equilibrium (Figure 3A). The addition to the classical model is that we also draw a line showing where the nutrient level is in equilibrium (dashed line in Figure 3A). This equilibrium line (nullcline) of the slow variable, nutrients, is a vertical line if we assume the equilibrium nutrient concentration to be independent of vegetation. In this case the classical predictions of the alternative stable states theory arise. If the external nutrient loading is increasing, the vertical nutrient nullcline will shift to the right (Figure 3C). This implies that the intersection with the folded line (and thus the equilibrium) will shift to the right. If the nullcline intersects the fold bifurcation (F_1), the vegetation-rich equilibrium disappears and a regime shift will occur in which the vegetation decreases and the water will become turbid. If the nutrient load is subsequently decreased, vegetation can recolonize at the other fold bifurcation (F_2) which is at a lower nutrient loading level, a phenomenon called hysteresis (Figure 3E). So far there is no difference with the alternative states theory.

Now suppose that vegetation has an impact on the nutrient retention such that more vegetation means a higher equilibrium nutrient level at a given external loading level (Figure 3B). We further assume that the setting of the nutrient equilibrium is slow relative to changes in vegetation. This seems a reasonable assumption as the response of lakes to changes in phosphorus loading is usually very slow due to a release of phosphorus from the sediment pool (Sas 1989; Carpenter 2005). Now it is easy to see that we can then get ''slow–fast limit cycles'' if the nutrient nullcline separates both stable states by intersecting in the unstable part of the catastrophe fold (Muratori and Rinaldi 1991). This cycle can be understood as follows. If vegetation biomass is high, the nutrient status of the lake is slowly increasing (as we are left of the P nullcline). Because vegetation biomass adjusts quickly to the appropriate equilibrium value, the system follows the upper branch of the catastrophe fold until the critical point H_1 (the former fold bifurcation F_1) where the vegetation collapses. As the vegetation cover is now low, the phosphorus load will decrease (as we are right of the P nullcline). Therefore the nutrient status of the lake is slowly moving to the lower critical point H_2 (the former fold bifurcation F_2) and the vegetation recovers.

Such cycles only occur over a limited range of nutrient loading. At low nutrient loadings there is a stable equilibrium in the upper branch of the catastrophe fold (Figure 3D, the left nutrient nullcline). With increasing nutrient loadings the system will become cyclic if the nutrient nullcline intersects the former right-hand fold bifurcation (H_1) and there is no other intersection with the lower branch of the catastrophe fold. Such a bifurcation where a small limit cycle appears is called a supercritical Hopf bifurcation (Figure 3F). The nutrient nullcline now intersects only in the former unstable branch of the catastrophe fold, and the system will be cyclic. Note that in this range an increase of nutrients is predicted to have hardly any effect on the model behavior. The cycles remain approximately the same in this range. However, if the nutrient nullcline intersects the other former fold bifurcation (H_2), the cycles disappear and the system becomes permanently turbid. Note that this system shows no hysteresis as when you reduce

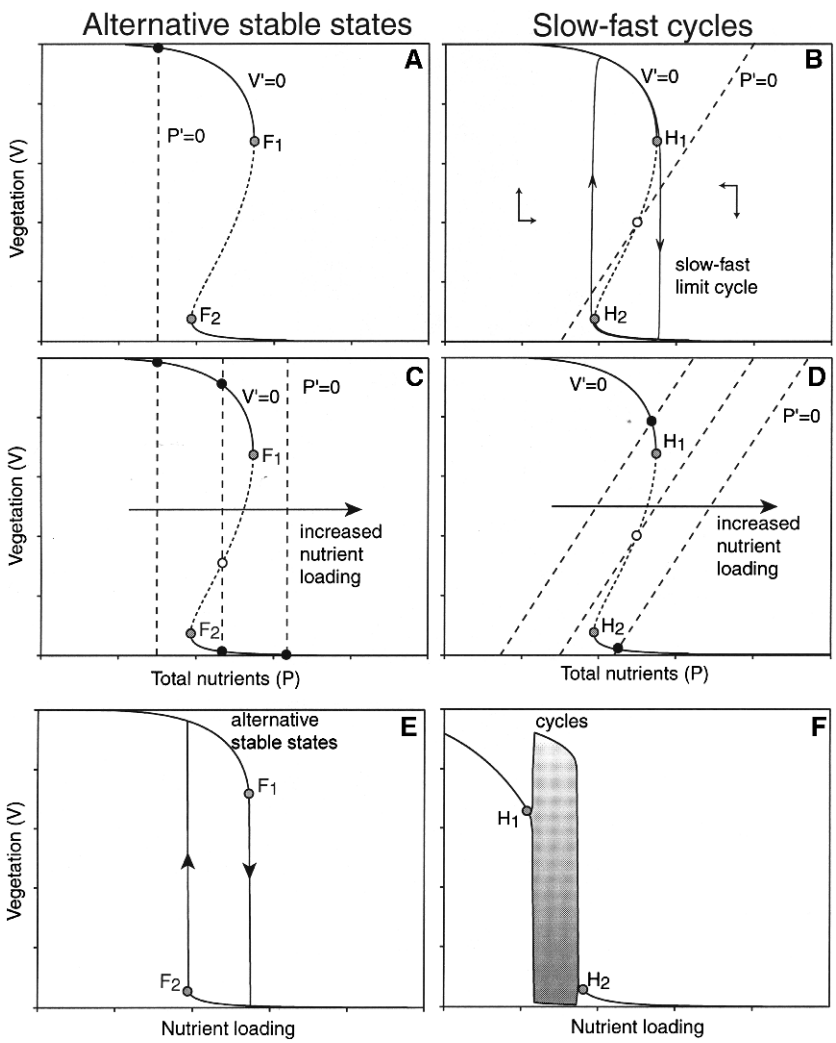

Figure 3. Graphical model to explain how a system with alternative equilibria can become cyclic if there is a long-term negative feedback (further explanation in text). (**A**) If vegetation has no negative effect on the phosphorus content in the lake, the system has alternative equilibria. (**B**) If vegetation has a negative effect and if the nutrient nullcline intersects the unstable part of the catastrophe fold, and the nutrient equilibrium sets slowly, there can be slow–fast cycles. (**C**) The system has alternative equilibria over a range of phosphorus loadings (F_1 and F_2 are fold bifurcations). (**D**) The system has cycles over a range of phosphorus loadings (H_1 and H_2 are Hopf bifurcations). (**E**) The effects of increasing and decreasing P loading on a system with alternative states. (**F**) The effect of P loading on a cyclic system.

the nutrient loading (Figure 3F), the system again becomes cyclic at the same critical point (H_2).

Simple Models of Two Different Potential Mechanisms

The above geometric analysis shows that cycles may occur if vegetation has a negative impact on a slowly responding nutrient status of the lake. Now we examine two potential mechanisms for this effect more closely. Our approach is to develop a simple dynamical model of each mechanism, and analyze both models to see whether these mechanisms might in principle explain the cycles observed in Lake Botshol.

Mechanism 1: Effect of Vegetation on Phosphorus Retention

The simplest mechanism we consider is straightforward loading and unloading of the phosphorus pool stored in a lake. Most lakes have a tendency to accumulate phosphorus as the concentration of the inflowing water is often higher than that of the water in the lake (and leaving the lake) (Vollenweider 1976). The mechanism is that part of the nutrients taken up by algae and other organisms end up buried with organic matter in the accumulating sediments. The net result is retention of phosphorus in the lake.

It has been shown that submerged macrophytes can greatly enhance the retention of phosphorus in lakes (Carpenter 1981; Scheffer 1998). As macrophytes have a clearing effect on the water column, they leave it with less phytoplankton and suspended sediments and generally with a much lower total-P concentration. This implies that the water flowing out of the lake carries less phosphorus away, implying that a clear and vegetated lake will retain more phosphorus than a turbid lake (assuming that the external load remail unaltered). Although most phosphorus is stored in the sedi-

ment, the amount available in the water phase will eventually increase too, as the sediment pool increases due to concentration dependent partitioning between the sediment and the water. This may invoke increased phytoplankton growth and push the system towards the turbid state in the long run.

We implement this mechanism in a vegetation model of Scheffer (1998) that describes the alternative stable states in shallow lakes. In this model the equilibrium vegetation cover (V) is assumed to be a sigmoidal function of the vertical light attenuation (E) (Scheffer 1998). If the light attenuation exceeds a certain threshold (h_E), a lake can get vegetated. Vegetation cover is assumed to grow logistically to this equilibrium:

$$\frac{\mathrm{d}V}{\mathrm{d}t} = r_V V\left(1 - \frac{V(h_E^{p_E} + E^{p_E})}{h_E^{p_E}}\right) \tag{1}$$

We assume for simplicity that the vertical light attenuation is a linear function of the total phosphorus of the water (P_w):

$$E = \gamma_E P_w \tag{2}$$

We further model the total phosphorus pool of the lake (P, g m^{-2}), which is the sum of the phosphorus available in the water phase (concentration P_w, g m^{-3} times mean depth z, m) and in the sediment. This pool is affected by the phosphorus concentration in the inflow ($P_{w,\mathrm{in}}$, g m^{-3}) and the residence time (τ). Part of the fraction in the sediment can be buried with a rate of (r_B) and become unavailable.

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{P_{w,\mathrm{in}} - P_w}{\tau} z - r_B(P - zP_w) \tag{3}$$

In this model we also assume that in the absence of vegetation a fixed fraction (c_P) of the total phosphorus content of the lake is in the water phase, but that vegetation alters the partioning between sediment and water due to the ''clearing effect'' of plants modeled as a Monod function with a half saturation constant of h_V:

$$P_w = \frac{P}{z} C_P \frac{h_V}{h_V + V} \tag{4}$$

In this way vegetation instantaneously reduces the phosphorus content of the water, which implies a direct positive feedback, as the plants grow better if turbidity is reduced. However, in the long run the reduced phosphorus content in the water outlet causes the total phosphorus content of the lake to increase slowly, which implies a simultaneous ''slow'' negative feedback.

Mechanism 2: Anoxic P Release on Accumulation of Organic Material

Although P release from the sediment should increase with the P content of the sediments, it may also vary widely depending on the redox conditions in the top sediment layer (Lijklema 1977). Anoxic conditions can boost sediment P release. It seems reasonable to expect that macrophyte dominance may under some conditions lead to accumulation of organic material and thus promote the chances of anoxia happening at the sediment surface. Moss and others (1990) and Perrow and others (1994) suggested that this mechanism might in fact explain cyclic vegetation patterns in Alderfen broad. In years with macrophyte domination, vegetation grows in summer and decays in winter. The decay of plant material is relatively slow and takes generally longer than one winter season (Godshalk and Wetzel 1978). Therefore, in consecutive years, an increasing pool of organic material from decomposing plants is built up (Asaeda and others 2000). As decomposition requires oxygen, the sediment can become anaerobic and P release from sediment can be boosted resulting in a potential shift to a turbid state.

To explore this mechanism, we model vegetation in a similar way as in the first model [equation (1)], but now we assume that vegetation can lead to an increase of sediment oxygen demand (SOD) due to accumulation of decaying organic material:

$$\frac{\mathrm{dSOD}}{\mathrm{d}t} = k_V V - l_{\mathrm{SOD}}\mathrm{SOD} \tag{5}$$

where k_V is a parameter describing the build-up due to vegetation and l_{SOD} is the first-order decay of SOD. We assume that there is a threshold (H_{SOD}) above which the SOD depletes oxygen in such way that there is a strong P flux from the anaerobic sediment (Moss and others 1990; Perrow and others 1994). For simplicity we assume the sediment phosphorus pool to be large and we only model the phosphorus in the water column. The total phosphorus in the water (P_w) now becomes:

$$\frac{\mathrm{d}P_w}{\mathrm{d}t} = \frac{P_{w,\mathrm{in}} - P_w}{\tau} + g\frac{\mathrm{SOD}^{p_{\mathrm{SOD}}}}{\mathrm{SOD}^{p_{\mathrm{SOD}}} + H_{\mathrm{SOD}}{}^{p_{\mathrm{SOD}}}} \tag{6}$$

p_{SOD} is a parameter that determines the steepness of the increase in sediment P release around the critical value H_{SOD} and g represents the maximum release rate. Following the reasoning explained for the first model [equations (2) and (4)], turbidity (E) depends on the phosphorus content of the water P_w but decreases with vegetation cover:

$$E = \gamma_E P_w \frac{h_V}{h_V + V} \tag{7}$$

Note that because we no longer simulate the total-P pool of the lake, we are now neglecting the effect of vegetation on P_w [as formulated in equations (3) and (4)]. In lakes with a long residence time, the dynamics of SOD is an order of magnitude faster than the dynamics of P_w. In such cases we simplify the model further by assuming that SOD is always at its equilibrium. SOD can then be expressed simply as a function of vegetation (obtained by setting equation (5) to zero). Equation (5) is thus replaced by the following function:

$$\mathrm{SOD} = \frac{k_V V}{l_{\mathrm{SOD}}} \tag{8}$$

We checked numerically for the default parameter settings that the resulting two-dimensional model has similar behavior as the three-dimensional model, but we found that the period of the cycles in the simplified model is approximately 20% faster. To compensate for this effect we scaled the time by a factor 0.8.

Methods of Analysis

We analyzed the sensitivity of cyclic behavior of the models to parameter changes, focusing on two aspects: (1) how the period of the cycles is affected by small parameter changes and (2) in what range of parameters the model behavior is cyclic. The effect on the length of the cycles is assessed by changing the value of each parameter in turn ± 10% and measuring the effect on the length of the period in days by simulation. A sensitivity coefficient was defined as the relative change of the length of the period of the cycle.

The range of parameters where the model behavior is periodic is assessed by one-dimensional bifurcation analyses for each parameter while keeping all other parameters to their default value. The bifurcation analyses were performed with the program LOCBIF (Khibnik and others 1992) for local bifurcations (Hopf bifurcation). We checked the models further for global bifurcations by simulation in MATLAB.

Parameter Estimation

As a basis of the parameterization of both models we fitted the vegetation nullcline of both models to Figure 2B to obtain a realistic range of alternative states. The relation between total P and vertical light attenuation (parameter γ_E) was fitted to measured data (Rip and others 2005). The hydraulic residence time (τ) was estimated based on the volume of the water and average inflow (unpublished data W.J. Rip). Some other parameters were hard to determine (for example, C_p, g, H_{SOD}). Here we either calibrated to get cyclic behavior, or took what seemed a reasonable value (Table 1). Burial of phosphorus in sediment (r_B) was neglected.

Model Results

As we neglected sediment burial of phosphorus in the first model, it can be shown easily from equations (3) and (4) that phosphorus nullcline is a straight line:

$$V^* = \frac{h_V C_p}{z\ P_{w,\mathrm{in}}} P^* - h_V \tag{9}$$

This situation is thus similar to the graphical model (Figure 3) and a crossing of both nullclines in the unstable part of the catastrophe fold is possible, depending on the parameters in the equation (10) (Fig. 4a). The maximum rate of change of the lake phosphorus pool is also much smaller than that of vegetation (a ratio of about 0.02 for default parameter settings), so both conditions for slow–fast cycles are fulfilled. If we run simulations we do indeed get cycles, but our simulations also reveal that the default parameters cause these cycles to have a very long period of about 27 years (Figure 4C).

The second model has a non-linear P_w nullcline (Figure 4B) (for convenience this nullcline is written as a function of vegetation V instead of P_w):

$$P_w^* = P_{w,\mathrm{in}} + \tau g \frac{(V^*)^{p_{\mathrm{SOD}}}}{(V^*)^{p_{\mathrm{SOD}}} + (H_{\mathrm{SOD}} l_{\mathrm{SOD}}/k_V)^{p_{\mathrm{SOD}}}} \tag{10}$$

The equilibrium phosphorus level thus equals the phosphorus level in the inflow plus a sigmoidal Hill function of vegetation cover. This formula illustrates that in the model the negative effect of vegetation on phosphorus only takes place above a certain level of vegetation. This nullcline can intersect the unstable part of the catastrophe fold. Moreover, the time scale of the phosphorus is also much slower than the vegetation (in a standard run a ratio of 0.005), so again the requirements for cycles are fulfilled as deduced from the slow–fast analysis. Indeed, simulations show cycles (Figure 4B,D). With the default parameter settings these cycles have a period of almost 5 years (Figure 4D), which is close to what is observed in Lake Botshol and Alderfen Broad. Moreover, the shape of the vegetation peak resembles the field pattern more closely.The sensitivity analysis of the parameters with regard to the period

Table 1. State Variables and Default Parameter Values of both Models

Parameter/state variable	Description	Default value	Ref.	Model
V	Fraction of the area of the lake covered with vegetation (–)	–	–	1,2
P	Total phosphorus pool in water and sediment (g m^{-2})	–	–	1
P_w	Total phosphorus concentration of the water (g m^{-3})	–	–	1,2
E	Vertical light attenuation (function of P_w) (m^{-1})	–	–	1,2
C_p	Partition of phosphorus over water and sediment	0.2		1
g	Maximal effect of SOD on phosphorus (g m^{-3} d^{-1})	0.002	(4)	2
γ_E	Relation between total P and light attenuation (m^2 g^{-1})	30	(3)	1,2
h_E	Light attenuation where half the lake is vegetated (m^{-1})	1	(5)	1,2
H_{SOD}	Critical sediment oxygen demand (g m^{-2})	2		2
h_v	Vegetation cover with half of the maximal effect on water clarity	0.2	(5)	1,2
k_V	Maximum attribution of vegetation to SOD (g m^{-2} d)	0.05	(5)	2
l_{SOD}	Mineralization rate of sediment oxygen demand (day)	0.01	(4)	2
p_E	Exponent in Hill function of positive vegetation effect	4	(2)	1,2
p_{SOD}	Exponent in Hill function for SOD effect on p_w	10	(4)	2
$P_{w,\text{in}}$	Phosphorus concentration incoming water divided by mean depth (g m^{-2})	0.05	(5)	1,2
r_B	Rate of phosphorus burial (d^{-1})	0	(4)	1
r_V	Maximum growth rate of vegetation (d^{-1})	0.07	(1)	1,2
τ	Retention time (day)	475	(3)	1,2
z	Mean water depth (m)	3	(3)	1,2

Model 1 is focusing on the loading of total phosphorus pool of the lake due to vegetation. Model 2 studies the hypothesis that vegetation causes an increase in the organic matter content of the sediment. (1) Van Nes and others (2003); (2) Scheffer (1998); (3) unpublished data Rip; (4) Assumed reasonable value; (5) Calibrated on Botshol data (Figure 2).

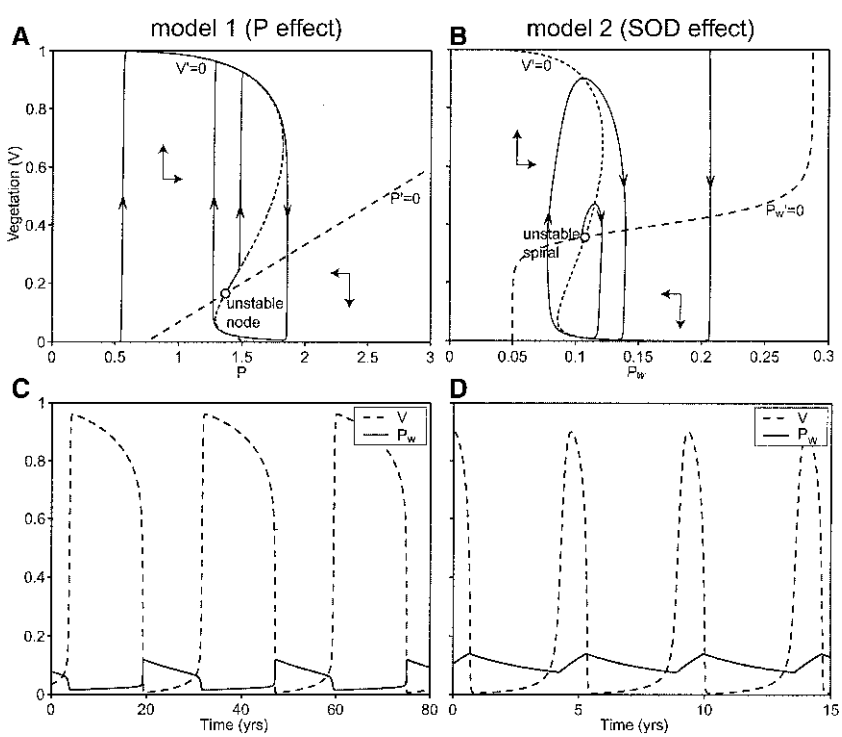

Figure 4. The dynamics of the two models. *Upper panels* (**A**, **B**) are the phase planes of both models with the nullclines for vegetation ($V' = 0$) and phosphorus ($P' = 0$ or $P_w' = 0$) and one trajectory (*solid line* with *arrows*). In the vegetated state, P is slowly increasing (see *horizontal arrows*) until the former critical threshold is passed, where the macrophytes collapse (see *vertical arrows*). As the P nullcline is crossed after the collapse of macrophytes, phosphorus will then slowly decrease again. This continues until the lower critical threshold is reached and vegetation can recolonize again (see also Figure 3). As the phosphorus dynamics are much slower than the vegetation dynamics, the cycle follows more or less the vegetation nullcline. The *lower panels* (**C**, **D**) show the time scale of the limit cycle of both models.

of the cycles (Table 2) shows that the exponent p_E and the parameter h_V have the largest effect in both models. These parameters determine the range of hysteresis in the model of Scheffer (1998). A larger hysteresis implies that the slowly changing phosphorus needs to be increased and decreased over a

longer range, which implies a longer period of the cycle. Another important parameter is the residence time (τ) in both models. This parameter determines the speed of the slow P content of the water (P_w) to a large extend. As these three important parameters (p_E, h_V and τ) were determined from data, we are relatively sure about the value of these parameters in Lake Botshol. In the first model, the partitioning of phosphorus also has a strong impact on the length of the cycles. This can be understood as this parameter determines the total amount of P stored in the lake. A lower C_p implies a higher total P pool in the sediment, which takes longer to load and unload. Unfortunately this parameter is quite unsure. However, we feel that our estimation of 20% of the phosphorus being in the water in the absence of vegetation is rather high. In reality C_p could be smaller, which means that our predicted cycle length for this model might be even longer, confirming that this mechanism is unlikely the main cause of the observed cycles.We further did one-dimensional bifurcation analyses for all parameters to find the ranges in which the model is cyclic. The first model always lost the cycles by means of a ''Hopf bifurcation'' which means that the amplitude of cycles becomes smaller until the cycles disappear. For all realistic values of some parameters (C_p and z), the model was cyclic. Other parameters had a quite small range where cycles occurred (for example, h_E and γ_E), but in general most parameters had a large range in which the model was cyclic, so the cycles seem to be a rather robust phenomenon. Of course this does not indicate that the phenomenon is also common in nature. Apart from uncertainties in the model, the default parameter setting might also be uncommon in real lakes.The second model sometimes has a special way of losing cycles with changing parameters. Instead of a gradually shrinking of the cycles (which occurs in a Hopf bifurcation), the period of the cycle becomes longer, while the amplitude hardly changes (Figure 5). This behavior can be understood from the nullclines. If the P_w nullcline moves to the right, it intersects with the lower bending point of the vegetation nullcline, creating a new equilibrium. Just after this first intersection, this equilibrium splits in two: a stable node and an unstable saddle point. But as the limit cycle is located very close to the vegetation nullcline these two equilibria will be part of the limit cycle. Because one equilibrium is stable the limit cycle will disappear at once (Figure 5A). A similar bifurcation can occur in the upper branch of the vegetation nullcline (Figure 5B). This global bifurcation is called an ''infinite-period bifurcation'' (Strogatz 1994). The biological implication is that with increasing nutrients the vegetated dominated state is predicted to alternate with increasingly longer periods without vegetation (Figure 5A,C). With decreasing nutrients the vegetated state will gradually become longer compared to the vegetationless state, until the vegetated state no longer alternates with periods without vegetation (Figure 5B,D).An important feature of the model is that it produces regular cycles if the external conditions remain unchanged. Even if some parameters are varied stochastically, the cycles of the model stay rather regular (not shown). This indicates that the regularity of the cycles in the field may be suggestive of such an intrinsic process if no obvious periodic external trigger is present. In the case of Alderfen Broad, no such external trigger is known. However, for the case of Lake Botshol, Ouboter and Rip (submitted) showed that there has been a remarkably regular pattern of wet and dry winters coinciding with the cycles in Lake Botshol. A wet winter results in a larger phosphorus load in summer than dry winters, as winter precipitation increases the phosphorus runoff from catchment areas. Perhaps, external forcing and internal feedbacks have interacted to drive the cycles in this case. As it seems unlikely that the precipitation cycle stays very regular, future development may shed more light on the relative role of climatic forcing.

Synthesis

In conclusion, our analyses suggest that cyclic shifts between alternative states may arise in shallow lakes as the result of a 'time-bomb effect' of slow internal eutrophication, followed by unloading. The cycles have the character of slow–fast limit cycles (Rinaldi and Scheffer 2000; Scheffer and Carpenter 2003) such as the ones described earlier for spruce budworm dynamics (May 1977; Ludwig and others 1978; Rinaldi and Muratori 1992a), elephant-fire oscillations (Dublin and others 1990) and predator prey systems (Rinaldi and Muratori 1992b). In all of these cases there is a positive feedback that could potentially cause alternative stable states, but the effect of this feedback is destabilized by a negative feedback that has a slower time scale (see Figure 6). This is analogous to the condition for self-organized pattern formation such as regular stripes (tiger bushes) labyrinths, spots (leopard bushes) or gaps (Rietkerk and others 2004). These patterns are also caused by a combination of a positive and a negative feedback, but the scale discrepancy between the two feedbacks is in space rather than in time.

Table 2. Sensitivity Analysis of Parameters of Model to the period and the Occurrence of Cycles of Both Models

	Period of cycles			Occurrence of cycles	
Parameter	Sensitivity −10%	Sensitivity +10%	Absolute average	Range of parameter	Bifurcations
Model 1					
C_p	0.10	−0.08	0.09	All realistic values	
γ_E	0.06	0.00	0.03	16.6–37.5	HH
h_E	0.00	0.05	0.03	0.8–1.8	HH
h_V	0.12	−0.10	0.11	<0.38	H
p_E	−0.17	0.15	0.16	2.4–8.9	HH
$P_{w,\mathrm{in}}$	0.06	0.00	0.03	0.03–0.06	HH
r_B	–	–	–	<0.8	H
r_V	0.01	−0.01	0.01	>0.0004	H
τ	−0.09	0.09	0.09	>3	H
z	0.00	0.00	0.00	All realistic values	
Model 2					
H_{SOD}	0.00	0.00	0.00	0.46–3.62	HH
$P_{w,\mathrm{in}}$	−0.05	0.06	0.06	<0.0859	I
g	0.02	−0.01	0.01	0.00015–1021	IH
γ_E	−0.03	0.05	0.04	12.7–51	II
h_E	0.06	−0.03	0.04	0.58–2.4	IH
h_V	0.07	−0.06	0.06	0.073–0.52	IH
kV	0.00	0.00	0.00	0.028–0.22	HH
l_{SOD}	0.00	0.00	0.00	0.0023–0.018	HH
p_E	−0.13	0.12	0.13	2.5–12.6	HI
p_{SOD}	0.00	0.00	0.00	>1.05	H
r_V	0.03	−0.02	0.03	>0.0032	H
τ	−0.06	0.06	0.06	>143.9	I

The sensitivity of the cycles is defined as the relative change of the period of the cycles if the parameter is change by ± 10%. The range of each parameter is determined by finding the bifurcations by increasing and decreasing the parameter in LOCBIF or MATLAB while all other parameters are at the default value (see: Table 1). H, Hopf bifurcation; I, infinite period bifurcation.

Our models suggest that cycles will only occur in particular cases. The singular perturbation theory analysis (Figure 3) implies that the nutrient nullcline should cross the vegetation nullcline in the unstable middle section of the fold. This happens only if: (1) the internal eutrophication effect of vegetation is relatively large; and (2) hysteresis in the system (considering nutrient level as a parameter, otherwise this term cannot be used) exists but is not too large. The latter can happen for instance in lakes that are not too shallow and where vegetation does not have a strong effect on clarity (Scheffer 1998; Van Nes and others 2002). The fact that particular conditions are needed for the cyclic behavior is in line with the apparent rarity of cyclic shifts in lakes. We are aware of only the two cases mentioned in this paper, despite the fact that numerous shallow lakes are monitored nowadays.

Although various parameters in our models are quite uncertain, our numerical results suggest that the simple increase of the phosphorus content of the sediment may be a too slow process to generate cycles of the observed frequency. By contrast accumulation of SOD resulting in anoxic sediment P release appears a candidate mechanism that may generate the cycles with frequencies corresponding to those observed in Lake Botshol and Alderfen Broad. However, it should be noted that although our models are simple, they have relatively many parameters, while our data sets are rather limited. Therefore it is possible that we got good results for the wrong reasons, for instance due to overfitting (Larimore and Mehra 1985). Clearly, the observed regular cycles in both lakes may always be due to a periodic external forcing. Nonetheless, our results suggest that periodic oscillations between a vegetated and a turbid state in shallow lakes may plausibly be explained from internal mechanisms. Similar intrinsic mechanisms, that undermine alternative states, could also occur in various other ecosystems with positive feedbacks.

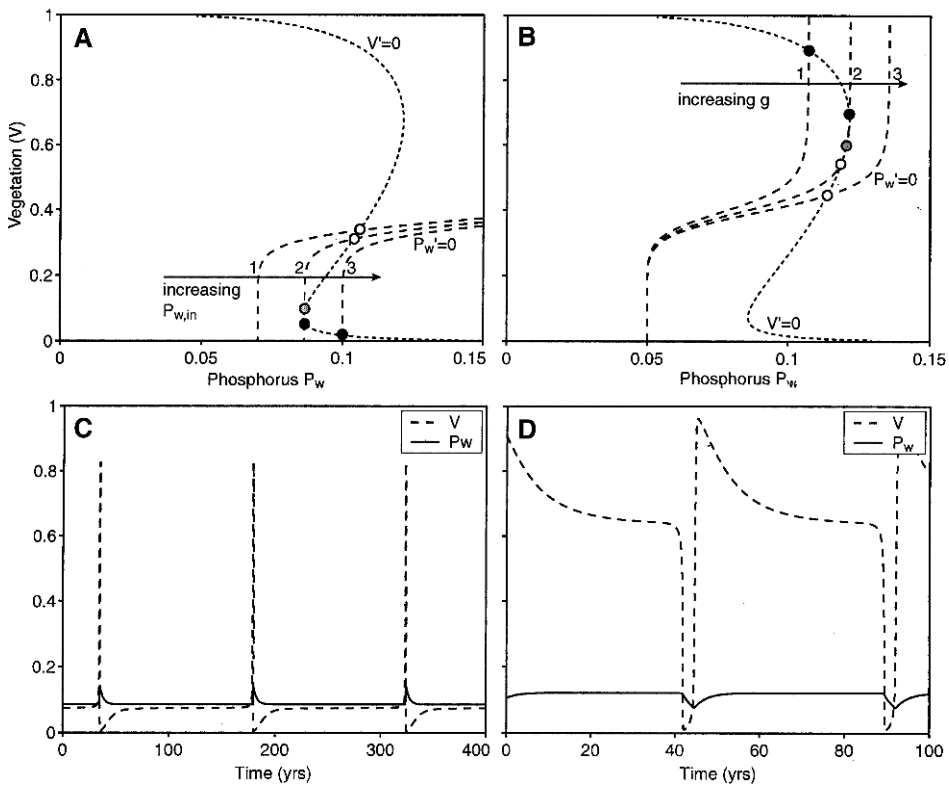

Figure 5. Two examples of obtaining an infinite-period bifurcation in the second model. At this bifurcation, an unstable saddle equilibrium (*gray circle*) and a stable node (*closed circle*) appear on a limit cycle with an unstable spiral (*open circle*). Close to the bifurcation point the cycles can become very long. (**A**) Nullclines at $P_{w,\mathrm{in}} = 0.007$ g m^{-3} (1), $P_{w,\mathrm{in}} = 0.0865$ g m^{-3} (2) and $P_{w,\mathrm{in}} = 0.01$ g m^{-3} (3) (**B**) Nullclines at $g = 0.00012$ g m^{-3} d^{-1} (1), $g = 0.000151$ g m^{-3} d^{-1} (2) and $g = 0.00018$ g m^{-3} d^{-1} (3). (**C**) Simulation at $P_{w,\mathrm{in}} = 0.0858899$ g m^{-3}. (**D**) Simulation at $g = 0.0001513415$ g m^{-3} d^{-1}.

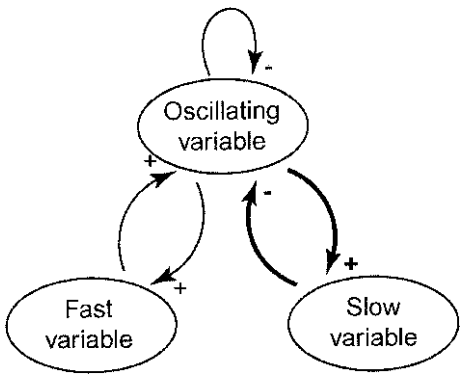

Figure 6. The feedbacks that may cause a variable to oscillate in slow–fast cycles. The oscillating variable (here: vegetation) has a positive feedback with a fast variable (here: turbidity) and a negative density dependence, which limits its growth. If the positive feedback is moderately strong it can cause the system to have alternative stable states. However if there is a third negative feedback, the dynamics of the system may change. This negative feedback can cause the system to become oscillating in a part of its parameter space if it involves a relatively slow variable (here; lake phosphorus) and if the effect of this feedback is relatively strong. If these conditions are not fulfilled, the negative feedback will simply reduce the strength of the positive feedback, and the alternative stable states may eventually disappear.

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REFERENCES

Asaeda T, Trung VK, Manatunge J. 2000. Modeling the effects of macrophyte growth and decomposition on the nutrient budget in shallow lakes. Aquat Bot 68:217–37.

Blindow I. 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshw Biol 28:15–27.

Blindow I, Andersson G, Hargeby A, Johansson S. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. Freshw Biol 30:159–67.

Blindow I, Hargeby A, Andersson G. 2002. Seasonal changes of mechanisms maintaining clear water in a shallow lake with abundant *Chara* vegetation. Aquat Bot 72:315–34.

Carpenter SR. 1981. Submersed vegetation: an internal factor in lake ecosystem succession. Am Nat 118:372–83.

Carpenter SR. 2005. Eutrophication of aquatic ecosystems: bistability and soil phosphorus. Proc Natl Acad Sci USA 102:10002–5.

Dublin HT, Sinclair AR, McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara Tanzania woodlands. J Anim Ecol 59:1147–64.

Godshalk GL, Wetzel RG. 1978. Decomposition of aquatic angiosperms. 2. Particulate components. Aquat Bot 5:301–27.

Khibnik AI, Kuznetsov YA, Levitin VV, Nikolaev EV. 1992. Continuation techniques and interactive software for bifurcation analysis of ODE's and iterative maps. Physica D 62:360–70.

Larimore WE, Mehra RK. 1985. The problem of overfitting data. Byte 10:167–78.

Lijklema L. 1977. The role of iron in the exchange of phosphate between water and sediments. In: Golterman HL, Ed. Interactions between sediments and freshwater. The Hague: Junk Publ. pp 313–7.

Ludwig D, Jones DD, Holling CS. 1978. Qualitative analysis of insect outbreak systems the spruce budworm and forest. J Anim Ecol 47:315–32.

May RM. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–7.

Meijer ML, De Boois I, Scheffer M, Portielje R, Hosper H. 1999. Biomanipulation in shallow lakes in The Netherlands: an evaluation of 18 case studies. Hydrobiologia 408/409:13–30.

Mitchell SF. 1989. Primary production in a shallow eutrophic lake dominated alternately by phytoplankton and by submerged macrophytes. Aquat Bot 33:101–10.

Moss B, Stansfield J, Irvine K. 1990. Problems in the restoration of a hypertrophic lake by diversion of a nutrient-rich inflow. Verh Int Ver Theor Angew Limnol 24:568–72.

Muratori S, Rinaldi S. 1991. A separation condition for existence of limit cycles in slow–fast systems. Appl Math Model 15:312–8.

Ouboter M, Rip WJ. 2006. Impact of meteorological fluctuations on P load of a shallow, restored lake in the Netherlands (submitted).

Perrow MR, Moss B, Stansfield J. 1994. Trophic interactions in a shallow lake following a reduction in nutrient loading—a long-term study. Hydrobiologia 276:43–52.

Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926–9.

Rinaldi S, Muratori S. 1992a. Limit cycles in slow–fast forest-pest models. Theor Popul Biol 41:26–43.

Rinaldi S, Muratori S. 1992b. Slow–fast limit cycles in predator-prey models. Ecol Model 61:287–308.

Rinaldi S, Scheffer M. 2000. Geometric analysis of ecological models with slow and fast processes. Ecosystems 3:507–21.

Rip WJ, Ouboter M, Beltman B, Van Nes EH. 2005. Oscillation of a shallow lake ecosystem upon reduction in external phosphorus load. Arch Hydrobiol 164:387–409.

Sas H. 1989. Lake restoration by reduction of nutrient loading: expectations, experiences, extrapolations. St Augustin: Academia Verlag Richarz.

Satake K. 1987. A small dredge for sampling aquatic macrophytes. Hydrobiologia 150:141–2.

Scheffer M. 1998. Ecology of shallow lakes. London: Chapman and Hall.

Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–56.

Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E. 1993. Alternative equilibria in shallow lakes. Trends Ecol Evol 8:275–9.

Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. Nature 413:591–6.

Shapiro J, Wright DL. 1984. Lake restoration by biomanipulation Round Lake, Minnesota, the first two years. Freshw Biol 14:371–84.

Simons J, Ohm M, Daalder R, Boers P, Rip W. 1994. Restoration of Botshol (the Netherlands) by reduction of external nutrient load -recovery of a characean community, dominated by *Chara connivens*. Hydrobiologia 276:243–53.

Strogatz SH. 1994. Nonlinear dynamics and chaos—with applications to physics, biology, chemistry and engineering. Reading: Addison-Wesley Publishing Company.

Van Geest GJ, Coops H, Scheffer M, van Nes EH. 2006. Transient macrophyte dominance in lakes with fluctuating water levels (this volume).

Van Nes EH, Scheffer M, Van den Berg MS, Coops H. 2002. Dominance of charophytes in eutrophic shallow lakes—when should we expect it to be an alternative stable state? Aquat Bot 72:275–96.

Van Nes EH, Scheffer M, Van den Berg MS, Coops H. 2003. Charisma: a spatial explicit simulation model of submerged macrophytes. Ecol Model 159:103–16.

Vollenweider RA. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell'Istituto Italiano di Idrobiologia 33:53–83.