EUTROPHICATION DUE TO PHOSPHORUS RECYCLING IN RELATION TO LAKE MORPHOMETRY, TEMPERATURE, AND MACROPHYTES

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Abstract. Lakes may have alternative states due to excessive phosphorus (P) input: a clear-water state and turbid one with high chlorophyll concentrations. Because shifts between these states have large ecosystem effects, and restoration after the shifts is costly or sometimes impossible, precise evaluation of the possibility of alternative states is needed for lake management. Yet the shifts are quite variable and seem to depend on many factors, including lake morphometry, temperature, and dominance of macrophytes. Here we evaluated the role of these factors using an empirically based model that included more mechanistic detail than earlier models of regime shifts in trophic state. Mean depth and temperature strongly influenced the susceptibility of lakes to regime shifts and lake restoration. The macrophyte effect of preventing P recycling from sediments was critical to the susceptibility of shallow lakes to regime shift. With warmer temperatures, eutrophication was more likely and restoration was less successful due to increased internal P recycling from the sediment. Lakes with intermediate depths were most susceptible to regime shifts and were least restorable. These lakes were too deep to be protected by macrophytes in their littoral zones and were too shallow to mitigate P recycling through hypolimnetic dilution. Our results illustrated the interplay of multiple physical, chemical, and biotic mechanisms in regime shifts, a complex type of causality that may arise in regime shifts of other types of ecosystems.

Key words: alternative states; eutrophication; lake management; lake morphometry; lake restoration; macrophytes; lake regime shift; phosphorus recycling; temperature; trophic status.

INTRODUCTION

Ecosystems are subject to shifts among multiple locally stable states (Holling 1973). Such regime shifts are fascinating ecological puzzles because they involve multiple causes, variables that change at different rates, and changes in direction of feedbacks (Scheffer et al. 2001*a*, Scheffer and Carpenter 2003). They are also crucial for ecosystem management because recovery of desired states may be difficult.

The shift from a condition of clear water to one with high concentrations of algal chlorophyll in lakes is among the best-studied examples of regime shifts. In shallow lakes, a shift from a state with clear water to another with turbid water may occur in response to increased nutrient loading and the substantial loss of macrophytes (e.g., Scheffer et al. 1993, Scheffer 1998). The clear-water state is characterized by dense macrophyte beds and low chlorophyll concentrations, while the turbid one exhibits sparse macrophyte beds and high chlorophyll concentrations. These transitions in shallow lakes are supported by diverse evidence and models (Jeppesen et al. 1998, Scheffer 1998). Even in deep, stratified lakes, alternative states in water clarity

are possible and related to phosphorus (P) recycling from sediments as controlled by oxygen concentrations in the hypolimnion (Carpenter et al. 1999, Carpenter 2003, Ludwig et al. 2003).

Inorganic P is bound to iron under oxic conditions and is released to the water when the hypolimnion is deoxygenated. One of the main causes of oxygen depletion in the hypolimnion is decomposition of sinking phytoplankton, which is related to lake trophic status. Elevated phytoplankton concentrations due to eutrophication lead to additional sedimentation that promotes bacterial respiration and anoxia. However, even if productivity in terms of total P or chlorophyll level is the same among lakes, P recycling may differ among ecosystems depending on factors that control hypolimnetic oxygen consumption, such as lake morphometry and hypolimnetic temperature (Charlton 1980). Such factors could cause great variability among lakes in the threshold for eutrophication.

Ecologists have used different models for regime shifts in shallow lakes (e.g., Scheffer 1998) or deep lakes (Carpenter 2003), reflecting the contrasting mechanisms that occur in the two categories of lakes. In nature, however, the categories are not so distinct, and lakes vary over continuous gradients of morphometry and mixing characteristics. Therefore, there is a need for models that can represent a wider variety of limnological conditions. Also, many of the existing models are rather abstract, with parameters that do not

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TABLE 1.   State variables, parameters, and their units as used in the model.

Symbol	Meaning	Units	Value (or range of values)	Source
State variables				
X	Chlorophyll concentration	µg chl/L		
P	Phosphorus concentration	µg P/L		
Parameters				
b	Algal growth rate per unit P	L·µg P^{-1}·d^{-1}	0.9†	Vanni et al. (1992)
g	Zooplankton grazing rate	d^{-1}	0.03	Beisner et al. (2003)
s	Algal sinking rate	m/d	0.085†	Vanni et al. (1992)
h	Flushing rate	d^{-1}	0.0006	Lathrop et al. (1998)
e	P excretion rate associated with grazing	µg P/µg chl	0.65†	Carpenter (1992)
l	P loading rate	µg P·L^{-1}·d^{-1}	0.02–0.5	Lathrop et al. (1998)
r	P recycling rate	µg P·L^{-1}·d^{-1}		Eq. 10
R	Areal P recycling rate	mg P·m^{-2}·d^{-1}		Eq. 4
A_p	Proportion of lake area without macrophytes	dimensionless		Eq. 9
z_e	Depth of thermocline	m		Eq. 3
z_h	Mean hypolimnion thickness	m		Eq. 8
z^*	Maximum depth of macrophyte distribution	m		Eq. 5
A_0	Lake area	km^2	0.01–1000	
$\bar{z}$	Mean depth	m	1–100	
T	Temperature (at the hypolimnion)	°C	4–20	

  † Values used here are the mean from values of two different algae, nanoplankton and blue-green algae, which were discriminated in the original literature.

directly represent observable properties of ecosystems. For example, the sigmoid model of P recycling contains a parameter (the half-saturation constant) that is difficult to estimate for most lakes and is probably a function of lake morphometry and water temperature (Carpenter 2003). We would prefer to have models with parameters that are stable for a wide variety of limnological conditions, and are readily estimated from available data.

These concerns are addressed by the model introduced in this paper. The model expresses the relationship between P input and chlorophyll concentration in terms of observed empirical relationships that incorporate effects of lake morphometry, macrophyte coverage, and water temperature. The model is used to investigate the conditions under which regime shifts can occur between clear-water and turbid conditions. The model reveals complex mechanisms that involve feedbacks among physical, chemical, and biotic processes. Surprisingly, lakes of intermediate depth prove most vulnerable to regime shifts, suggesting that such lakes should be a priority for management efforts.

MODEL DESCRIPTION

Basic model

The basic model is composed of two dynamic variables in the epilimnion: algal density (X) and P concentration (P):

$$\frac{dX}{dt} = bPX - \left(g + \frac{s}{z_e} + h\right)X \qquad (1)$$

$$\frac{dP}{dt} = l + r + egX - bXP - hP. \qquad (2)$$

The meanings and units of the variables and parameters are listed in Table 1. The dynamics of these variables can be divided into two processes: inputs (positive signs) and outputs (negative signs).

Algae grow at a rate b and disappear due to grazing by zooplankton (g), sinking (s/z_e), and flushing (h). The sinking loss (d^{-1}) is the sinking velocity of algae, s (m/d), divided by the thickness of the epilimnion, z_e (m). The epilimnion thickness is determined by the empirical lake area–thermocline depth relationship (Hanna 1990):

$$z_c = 6.95\,(A_0)^{0.185} \qquad (3)$$

where A_0 is the lake area (km^2).

Inputs of P include P loading from the watershed (l) and P recycling from the sediment (r). We regard this P loading as controllable inputs in terms of restoration management. For this reason, there is a minimum value, l_{min}, which represents uncontrollable inputs such as dry fallout, precipitation, and groundwater. According to the estimated value in Lake Mendota (Wisconsin, USA; Lathrop et al. 1998), we set $l_{min} = 0.02$ µg P·L^{-1}·d^{-1}. We assume that P uptake of algae by zooplankton is incomplete, so that P is released into the epilimnion at a rate e when algae are grazed by zooplankton. Losses of P include sequestration in algae and flushing. Here P consumed by algae was converted to chlorophyll assuming a ratio of unity by mass (Reynolds 1984).

P recycling from the sediment

We assume that P recycling from the sediment does not occur when the hypolimnion is oxic and that recycling occurs at the mean rate reported by Nürnberg (1984), 14 mg P·m^{-2}·d^{-1}, when anoxic. We assume that the input of the recycled P from the hypolimnion into

the epilimnion occurs at the maximal rate, 14 mg $P \cdot m^{-2} \cdot d^{-1}$, times the proportion of anoxic days in the hypolimnion during the stratified season, which is assumed 150 d long. This assumption arises because we are interested in the mean summer bloom of algae, rather than seasonal or daily changes in algal density. To quantify anoxia in the hypolimnion, we use an oxygen depletion rate that is a function of chlorophyll concentration, hypolimnion thickness, and hypolimnion temperature (Charlton 1980). Thus, the full expression of areal P recycling into the epilimnion, R (mg $P \cdot m^{-2} \cdot d^{-1}$), based on the Charlton (1980) model is

$$R = \frac{14}{150} \times \left[150 - \frac{DO \times (50 + z_h)}{3.8 \times f(X) \times k(T) + \alpha} \right] \quad (4)$$

where $f(X) = 1.15 \, X^{1.33}/(9 + 1.15 \, X^{1.33})$, $k(T) = 2^{(T-4)/10}$, and $\alpha = 0.12$. As for DO, we used the saturated oxygen concentration corresponding to each temperature (T) as the initial concentration in the hypolimnion. The R value can be negative under conditions of low chlorophyll concentration, low temperature, and deep hypolimnion thickness. When R takes a negative value, we set it equal to 0.

Effects of macrophytes

One of the major factors in determining macrophyte distribution is light availability (Spence 1982). Since macrophytes grow on the sediment in lakes, they are likely to be affected by overlying light conditions. The relationship between light availability and maximum depth of macrophyte distribution (z^*) is among the most clearly documented effects of the environmental conditions on macrophytes. However, the effect of light on macrophyte density can be more complicated, depending on other conditions such as steepness of littoral slope (Duarte and Kalff 1986). By combining the z^*–Secchi depth (Duarte and Kalff 1990) and Secchi depth–chlorophyll (Carlson 1977) relationships, we obtain

$$z^* = 1.9 + 4.85 \, X^{-0.68}. \quad (5)$$

We assume that macrophytes are able to root only in the epilimnetic zone (i.e., $z^* \leq z_e$). Macrophytes decrease P recycling from sediments (Scheffer 1998). For simplicity, we assume that P recycling does not occur from the part of the sediment where macrophytes root. The model was run with and without macrophytes separately to look at the effects of the presence of macrophytes.

Lake morphometry

Lake basins can be modeled by quadric surfaces or sinusoids (Carpenter 1983). In this article we adopt quadric surfaces for the shapes of lakes, because they are mathematically easier to handle and could be applied to most lakes in terms of the depth ratio ($\bar{z}/z_m$, ratio of mean depth to maximum depth). The depth ratio of quadric surfaces takes a range 0.33–0.66, while

that of sinusoids is 0.297–0.5 (Carpenter 1983). Quadric surfaces include lakes with flat bottoms (large depth ratios), as well as typical glacial lakes that have gradual littoral slopes and deep central basins (small depth ratios). The proportions of the lake's surface area that encompasses water depths shallower than z, $A(z)$, and the lake's volume that lies above depth z, $V(z)$, which are completely determined by the depth ratio and maximum depth, are estimated as

$$A(z) = 3 \times \left(2 \times \frac{\bar{z}}{z_m} - 1 \right) \times \left(\frac{z}{z_m} \right)^2$$
$$- 2 \times \left(3 \times \frac{\bar{z}}{z_m} - 2 \right) \times \frac{z}{z_m} \quad (6)$$

$$V(z) = \left[\frac{z}{z_m} + \left(3 \times \frac{\bar{z}}{z_m} - 2 \right) \times \left(\frac{z}{z_m} \right)^2 \right.$$
$$\left. - \left(2 \times \frac{\bar{z}}{z_m} - 1 \right) \times \left(\frac{z}{z_m} \right)^3 \right] \bigg/ \left(\frac{\bar{z}}{z_m} \right) \quad (7)$$

respectively (Carpenter 1983).

We use lake area (A_0), mean depth ($\bar{z}$), and depth ratio to look into the effects of lake morphometry on the tendency of ecosystems to undergo regime shift. Because the depth ratio includes only two elements, mean depth ($\bar{z}$) and maximum depth (z_m), we only varied z_m and left $\bar{z}$ unchanged. Lake area affects the thermocline depth (Eq. 3), therefore it is theoretically possible for the thermocline depth to exceed the lake's maximum depth. In this case, there is no hypolimnion and $z_e = z_m$, and we assume that T corresponds to the temperature near the lake's bottom. When $z_e < z_m$, the mean hypolimnion thickness, z_h, is given by

$$z_h = \frac{1 - V(z_e)}{A(z_e)} \times \bar{z}. \quad (8)$$

The proportion of the sediment without macrophytes, A_p, where P recycling can occur, is given by

$$A_p = 1 - A(z^*). \quad (9)$$

In a lake where the maximum depth of macrophyte distribution (z^*) obtained by Eq. 5 is deeper than the lake's maximum depth, the lake is assumed to be completely covered by macrophytes and $A_p = 0$. The volumetric P recycling from the sediment into the epilimnion, r, is represented by

$$r = A_p \cdot R/z_e. \quad (10)$$

Eq. 10 is based on the assumptions that (1) P release from sediments in the epilimnetic zone cannot be distinguished from P release from anoxic hypolimnia (Kalff 2002), and (2) P releases from epilimnetic sediments depend on algal density and temperature, as is assumed for the hypolimnetic P release.

P loading and equilibria

The equilibria of the model are obtained from Eqs. 1 and 2. The equilibrium P concentration (P^*) is given from Eq. 1 by the following equation:

$$P^* = \frac{1}{b}\left(g + \frac{s}{z_e} + h\right) \qquad (11)$$

which is independent of l and r. The equilibrium chlorophyll concentration (X^*) was calculated numerically by checking the sign of the right-hand side of Eq. 2, with X values increasing from $X = 0$ in increments of 0.01. An equilibrium value of X was attained for each case in which the new X value changed the sign of dP/dt. This iteration was repeated until X took its maximum value at $X_{max} = (l_{max} + r_{max}/z_e)/(aP^* - eg)$, where $l_{max} = 0.5$ and r_{max} was given by Eq. 4 with $f(X \to \infty) = 1$ and Eq. 10. For a given l value, this iteration yielded either a single stable equilibrium (the sign changed once), or three equilibria (the sign changed three times). In the case of multiple equilibria, one equilibrium had low chlorophyll concentration, the other high chlorophyll concentration, with the unstable equilibrium in between. To determine the reversibility of a lake, l was increased from $l_{min} = 0.02$ to 0.5 by 0.01 in the eutrophication process and this procedure was reversed in the restoration process. We defined the lakes as: reversible, when no multiple equilibria were obtained; hysteretic, when multiple equilibria were obtained except for $l = l_{min}$; and irreversible, when multiple equilibria were obtained for $l = l_{min}$.

RESULTS

Response of lakes to restoration by P reduction

Our empirically based model, like previous models (e.g., Carpenter et al. 1999), demonstrated alternative states of lake water clarity arose from excessive P input (Fig. 1). A shift between a clear-water state and a turbid state due to excessive P input can occur depending on lake morphometry and temperature in both lakes without macrophytes ($A_p = 1$) and with them (A_p is given by Eq. 9). The response of eutrophic lakes to reduced P input (e.g., management) exhibited three patterns depending on lake morphometry and temperature: reversible (Fig. 1A, D), hysteretic (Fig. 1B, E), and irreversible (Fig. 1C, F). Hereafter we refer to these as the lake response types. When a lake with macrophytes was categorized as a hysteretic (Fig. 1E) or irreversible (Fig. 1F) type, the solution differed between the process of eutrophication (solid line and closed circles) and restoration (dashed line and open circles). It was possible that even if a lake was predicted to be hysteretic, the lake might be unable to recover once it shifted to a turbid state (Fig. 1F). Such lack of response may arise because of the unidirectional competition for light between phytoplankton and macrophytes. As long as phytoplankton were not abundant and water was clear, macrophytes were abundant down to a considerable depth. However, once phytoplankton became abundant due to P input, the distribution of macrophytes was restricted to a very shallow zone, and their capacity to suppress P recycling was weaker.
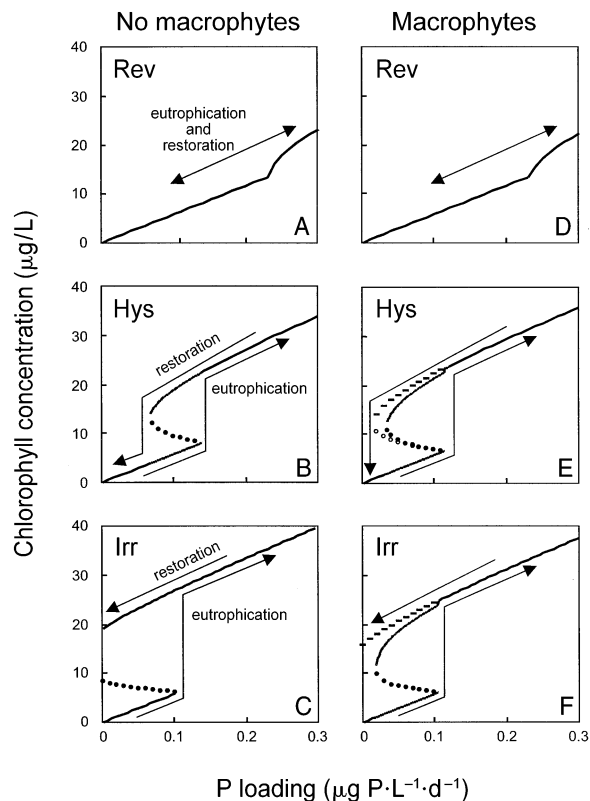

FIG. 1. Response types of lakes to eutrophication and restoration in terms of chlorophyll concentration along a gradient of P loading (A–C) without macrophytes ($A_p = 0$) and (D–E) with macrophytes (A_p is given by Eq. 9): (A, D) Rev, reversible type; (B, E) Hys, hysteretic type; (C, F) Irr, irreversible type. Different temperature values are used to create these panels: (A, D) $T = 9$; (B) $T = 11$; (E) $T = 12$; (C, F) $T = 12.5$. In all panels, $A_0 = 40$, $\bar{z} = 12.7$, and $z_m = 25.3$ (depth ratio = 0.5) were used.

Effects of morphometry and temperature on lake responses

Lake response types were not sensitive to changing lake area (A_0), regardless of the presence or absence of macrophytes (Fig. 2). In a deep lake with a hypolimnion, a larger area leads to a thicker epilimnion (Eq. 3). Consequently, a lake with a larger area had a thicker epilimnion and a thinner hypolimnion than a lake with smaller area and the same mean depth. These two morphological effects offset each other because a thicker epilimnion diluted recycled P (Eq. 10), whereas a thinner hypolimnion promoted more P recycling (Eq. 4). In a shallow lake where the entire water column was included in the epilimnion ($z_e = z_m$), lake area did not affect any parameters. Depth ratio had no remarkable effect on lake response types even if two extreme depth ratios (e.g., 0.33 and 0.66) were compared (*data not shown*). For these reasons, the lake area (40 km²) and depth ratio (0.5) of Lake Mendota were used as the representatives for later analyses unless otherwise stated.
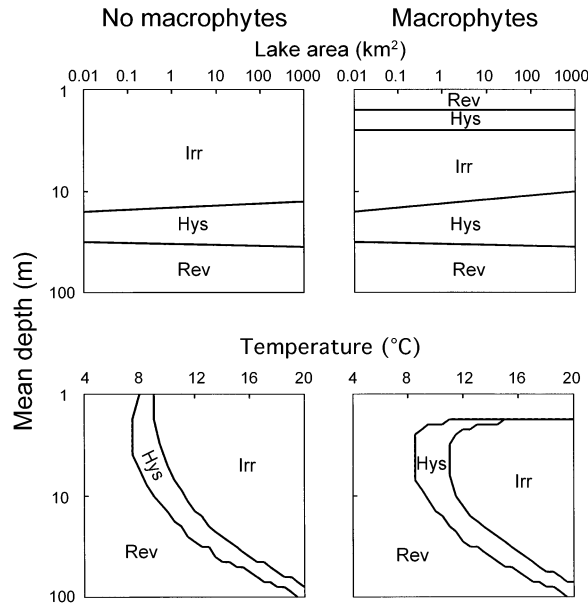
FIG. 2. Lake response types as affected by lake area, mean depth, and temperature in the absence (left panels) and presence (right panels) of macrophytes. In the upper panels (area vs. mean depth), the temperature is set at $T = 12$; in the lower panels (temperature vs. mean depth), the area is set at $A_0 = 40$. The depth ratio is 0.5. See Fig. 1 legend for key to abbreviations.

Lake response types were affected considerably by mean depth and temperature, and were different between lakes with macrophytes and those without them (Fig. 2). In a lake without macrophytes, the lake switched to more vulnerable types in terms of restoration management (i.e., hysteretic and irreversible) as the lake became shallower and warmer, mainly due to increased P recycling (Eq. 4). Even at a fixed temperature, the lake was less likely to exhibit hysteresis or irreversible shift when the lake was deeper (except for shallow lakes with macrophytes).

The presence of macrophytes apparently determined the likelihood of regime shift in shallow lakes (Fig. 2). For example, in the most shallow lakes the effect of macrophytes on reduction in P recycling from the sediment became stronger with decreasing mean depth, resulting in a low tendency towards irreversible shift. By contrast, no remarkable effect of macrophytes was found for deep lakes (>10 m). Because of the interaction between the effects of P recycling and macrophytes, macrophyte-rich lakes of intermediate mean depth were prone to severe regime shifts (i.e., irreversible type). In sum, in the presence of macrophytes the irreversible type was most likely for lakes with high temperature in the hypolimnion and intermediate mean depth (~10 m).

Hysteretic and irreversible types arose from P recycling from the sediment. Phosphorus recycling occurred when R took a positive value in Eq. 4, depending on chlorophyll concentration, mean depth and temper-ature (Fig. 3). The critical chlorophyll concentration above which P recycling occurred was lower with higher temperature, indicating that P recycling in warm lakes was likely even with low algal densities. There was also a critical mean depth for each temperature above which P recycling did not occur even with extremely high algal densities: this critical mean depth became deeper with increasing temperature.

Sensitivity of lakes to regime shifts

Regime shifts were characterized by four values that were sensitive to lake morphometry and temperature (Fig. 4A); the range of P loading in which a lake was subject to more than one state ($l_1 - l_2$), and the magnitude of the change in chlorophyll concentration after shift from clear (X_c) to turbid states (X_t). The l_1 value represents the threshold above which the lake can shift from a clear-water state to a turbid one by a disturbance independent of P input. The l_2 value represents the threshold above which a regime shift occurs without any other forces. When the difference between the states (X_c and X_t) is greater, the regime shift is larger.

These four values (l_1, l_2, X_c, X_t) were obtained by considering the input ($l + r + egX$ in Eq. 2; solid lines in Fig. 4B–D) and output lines ($bXP + hP$; broken lines). The vertical displacement of the input line increased with increasing P input l (Fig. 4B to C to D), while the output line remained constant. At $l = l_1$ (Fig. 4A, B), there were two equilibria with the lower one being stable and the upper one being unstable. When $l_1 < l < l_2$ (Fig. 4A, C), there were three equilibria with the lower and upper ones being stable and the one in between being unstable. At $l = l_2$ (Fig. 4A, D), there were two equilibria with the upper one being stable and the lower one being unstable. Note that it depended on the nonlinearity of the P recycling term r (corresponding to the steepness of the nonlinear parts of the input lines in Fig. 4B, C, D) whether the system had alternative states.

The l_1 value cannot be obtained analytically, because it depends on the nonlinearity of the P recycling (Fig.
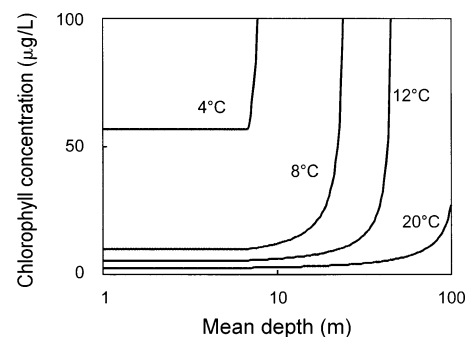

FIG. 3. Relationships between the lake's mean depth and the critical chlorophyll concentration, above which P recycling from the sediment occurs, with different temperature. Lake area is set at $A_0 = 40$.
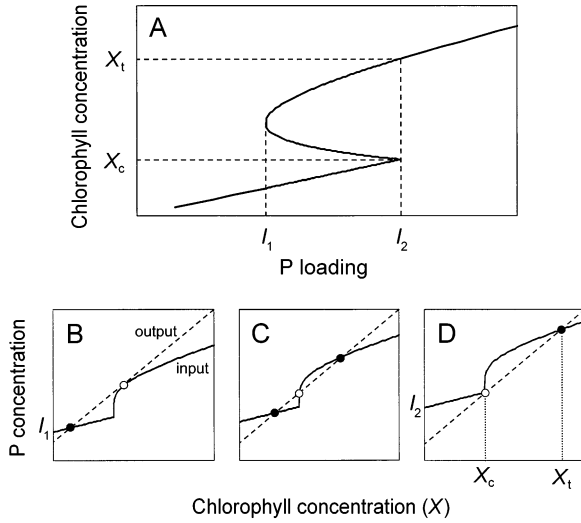
FIG. 4. (A) Schematic diagram showing values characteristic to regime shifts. A lake has potentially three equilibrium states with regard to chlorophyll concentration above a critical value of P loading (l_1). A regime shift from a clear-water state (X_c) to a turbid state (X_t) occurs when P loading exceeds another critical value (l_2). (B, C, D) Phosphorus input (solid lines) and output (broken lines) rates, according to Eq. 2, vs. chlorophyll. Closed circles denote stable equilibria, and open circles denote unstable equilibria. (B) The P loading is at the critical value, l_1, above which the lake has potentially three equilibria. (C) The lake has three equilibria. The lower and upper equilibria are stable, while the equilibrium in between is unstable. (D) The P loading is at the critical value, l_2, above which the lake shifts from a clear-water state (X_c) to a turbid state (X_t).

4B). The l_2 and X_c values were independent of the non-linearity in P recycling (Fig. 4D). X_c is the critical chlorophyll concentration with which $R = 0$ in Eq. 4. Thus X_c was obtained by the following equation:

$$f(X_c) = \frac{DO \times (50 + z_h)}{150 \times 3.8 \times k(T)}. \quad (12)$$

The l_2 value is obtained by

$$l_2 + egX_c = bX_cP^* + hP^* \quad (13)$$

where P^* denotes the equilibrium P concentration given in Eq. 11. The left-hand side of Eq. 13 represents the input terms (with $R = r = 0$) in Eq. 2 and the right-hand side the output terms. Rearranging Eq. 13, we have

$$l_2 = (bP^* - eg)X_c + hP^*. \quad (14)$$

Here we briefly note the dependence of the upper critical value for P loading (l_2) on some important limnological conditions. This dependence differed slightly between deep lakes that had a hypolimnion and shallow lakes that did not. For deep lakes with hypolimnion, the critical value became greater with colder water temperature (T), smaller area (A_0), or deeper mean depth ($\bar{z}$). For shallow lakes without hypolimnion, it became greater with colder temperature or shallower mean

depth. As for X_t, this value was dependent on the non-linearity in P recycling (Fig. 4D).

The interaction between the range of P loading to induce a regime shift and the magnitude of the resultant shift was dependent on lake area, mean depth, and temperature. A lake with a larger area was more likely to shift from a clear-water state to a turbid one at smaller P loading (smaller l_2), but the algal density after the shift was lower (smaller X_t) than for a small lake (Fig. 5A). Analyses revealed that regime shifts were likely in lakes with intermediate mean depth (1.9–28 m) when macrophytes were present (Fig. 5B), while in the absence of macrophytes (crosses in Fig. 5B), regime shifts were probable also for shallow lakes (<1.9 m). Increasing temperature brought about smaller l_1 and l_2 values and a greater difference between X_c and X_t (Fig. 5C). This means that a regime shift is likely at a lower P loading level and that the shift from a clear-water state to a turbid one is likely to be more drastic in a warmer lake.

Application of the model to Lake Mendota showed that both morphometry and temperature influenced algal–macrophyte interactions (Fig. 6). Lake Mendota is 40 km² in lake area, 12.7 m in mean depth, 25.3 m in maximum depth (depth ratio = 0.5) and has a mean P loading of 0.18 μg P·L⁻¹·d⁻¹ (Lathrop et al. 1998). We assumed that the hypolimnion temperature was 12°C although the temperature in the summer time varies among years. If Lake Mendota were smaller than 0.67 km² in area and the other morphometrical parameters and the temperature were the same as its original values, the lake would still remain in a clear-water state (Fig. 6A) because of the higher critical P loading required for an unforced regime shift in small lakes ($l_2 > 0.18$; Fig. 5A). However, a regime shift could occur if P loading increased beyond the critical l_2 values even in lakes <0.67 km². If the lake were shallower than 2 m or deeper than 24 m, the lake would remain in a clear-water state due to l_2 values higher than 0.18 regardless of the macrophyte effect (Fig. 6B). In between (2–24 m), the difference in chlorophyll concentration between lakes with and without macrophytes diminished with increased mean depth. Lakes with temperature lower than 9°C were categorized as reversible (Fig. 6C), while increases in temperature led to increases in algal density as was clear from the increases in X_t with temperature in Fig. 5C. The predicted chlorophyll concentration, 28 μg/L, from the model with the morphometry and temperature (12°C) of Lake Mendota at the mean P loading (0.18 μg P·L⁻¹·d⁻¹) was in good accord with the field values (Brock 1985).

Sensitivity analyses of the model outcome

Like any simulation, our empirically based recycling model was subject to uncertainties that may influence predictions of lake response to P loading. For example, we assumed that P recycling did not occur from the part of the sediment covered by macrophytes (Fig. 2).
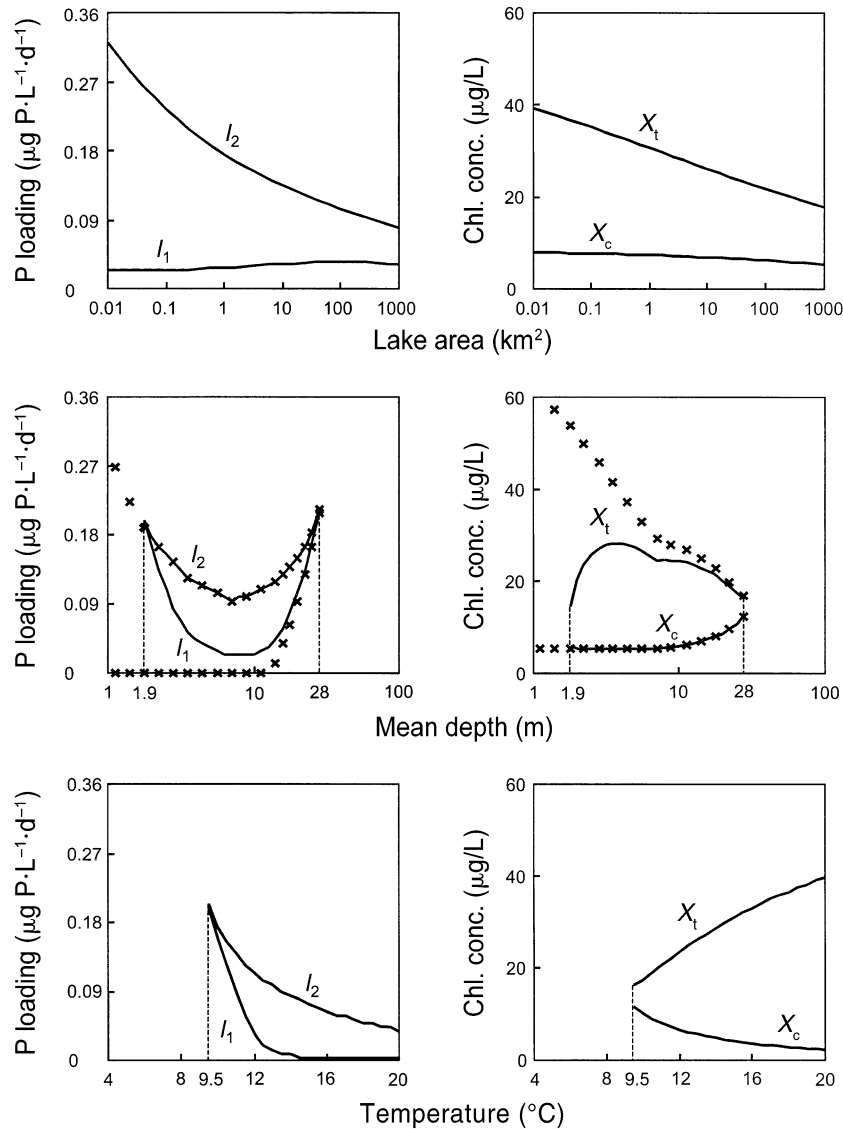
FIG. 5. Diagrams showing the susceptibility of lakes with macrophytes to alternative states and regime shifts (l_1 and l_2 values; left panels) and the chlorophyll concentration before and after a regime shift (X_c and X_t values; right panels) vs. area, mean depth, and temperature. (Top panels) Effects of changing lake area on the l_1, l_2, X_c and X_t values defined in Fig. 4A. (Middle panels) Effects of mean depth. The case for lakes without macrophytes is also plotted (×). (Bottom panels) Effects of changing temperature. In these simulations, $A_0 = 40$, $\bar{z} = 12.7$, $z_m = 25.3$, and $T = 12$ were used unless otherwise stated.

However, sensitivity analysis revealed that the model outcome was affected qualitatively and quantitatively by the degree to which macrophytes reduced P recycling from the sediment covered by beds of the plants (Fig. 7). For example, macrophytes were still effective when P recycling was reduced 90% by the plants, but even shallow lakes (~1 m) could not be reversible (without hysteresis) at 12°C and higher. At 50% reduction, the effect of macrophytes diminished considerably: even shallow lakes were irreversible with temperature >10.5°C. Thus effectiveness of macrophytes in reducing P recycling and temperature were critical to the prediction.

We also tested the robustness of the assumption that P recycling occurred at the mean rate of 14 mg P·m^{-2}·d^{-1} under anoxic conditions (Nürnberg 1984) by changing the rate within the range of its standard deviation (6.8 mg P·m^{-2}·d^{-1}). Overall, the model outcome was insensitive to this assumption, although the hysteretic and irreversible regions in the presence of macrophytes became wider with a higher P recycling rate, while shallow lakes (<1.9 m in mean depth) remained reversible.

Although Eq. 5 followed empirical relationships, one may question the implication that there was no chlorophyll concentration that was sufficient to eliminate
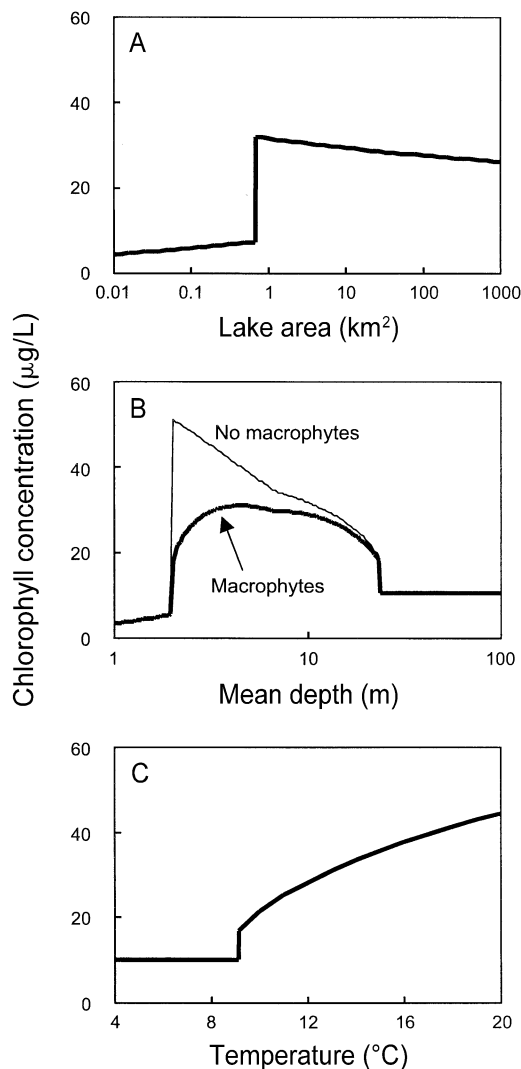
Chlorophyll concentration (μg/L)

FIG. 6. The effect of changes in morphometry or temperature on the chlorophyll concentration predicted by the model with macrophytes, in the current Lake Mendota (Wisconsin) condition ($A_0 = 40$, $\bar{z} = 12.7$, $z_m = 25.3$, $T = 12$, $l = 0.18$). (A) Lake area is varied from that of Lake Mendota. (B) Mean depth is varied. The case without macrophytes is also indicated (thin line). (C) Temperature is varied.

macrophytes from shallow waters (<1.9 m). When this effect was removed (i.e., $z^* = 4.85\ X^{-0.68}$), lakes with intermediate depths remained likely to be hysteretic or irreversible in the presence of macrophytes. However, the critical mean depth below which a lake was reversible declined to 0.7 m.

Finally, model outcome was not sensitive to the grazing rate (g) within the range (0.03–0.05) estimated by Beisner et al. (2003) nor to the flushing rate (h) when varied over a 10-fold range.

DISCUSSION

Our empirically derived model demonstrated that mean depth and temperature were critical in determining the reversibility of regime shift arising from eutrophication. In contrast, lake area had little effect on ecosystem tendency to undergo a regime shift. In general, lakes with larger area are also deeper than smaller ones (Hayes 1957), but the importance of mean depth among morphometrical characteristics should be mentioned separately because of exceptions such as Lake Chad in Africa (16 500 km² in area, ~1.5 m in mean depth). The strong effect of mean depth on regime shift arose from factors that mitigated P recycling from the hypolimnion. The effects of macrophytes were also closely associated with mean depth and were stronger in shallower lakes (Figs. 2 and 5B), reflecting their distribution restricted to the littoral zone. Temperature was an important, but usually uncontrollable, factor influencing regime shift. Increasing temperature always caused restoration to be more difficult (Fig. 2) and eutrophication to be more likely (Fig. 6C). Moreover, regime shifts were likely to take place at lower critical values of P loading (l_1 and l_2) and effects of regime shifts ($X_c - X_t$) would be larger in warm lakes (Fig. 5C). Unfortunately, temperature cannot be effectively regulated through common management strategies. Overall, the predicted effects of morphometry and temperature were consistent with empirical work in which
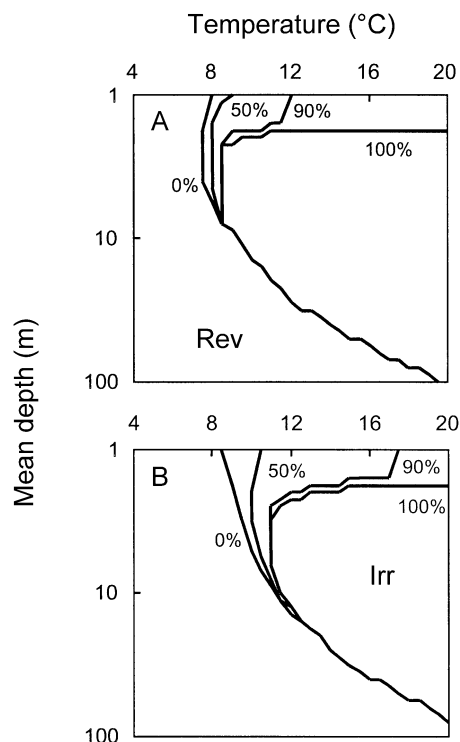

FIG. 7. Contour plots showing the effects of changing macrophyte efficiency on reducing P recycling from the sediment in the region of (A) reversible and (B) irreversible types. Note that, in panel (A), regions to the left of each plot line represent reversible lakes (Rev); in panel (B), regions to the right of each plot line represent irreversible ones (Irr).

the relationships between trophic status and hypolimnetic anoxia were studied (Cornett and Rigler 1980).

Sensitivity analyses suggested that the effectiveness of macrophytes in regulating P recycling was a critical factor influencing model predictions of ecosystem regime shift. Unfortunately, there is little consensus within the literature concerning how macrophytes affect nutrient recycling. For example, *Chara*, an evergreen species that exhibits slow decomposition, is associated with extremely low P release from sediment (Kufel and Kufel 2002) and *Hydrilla verticillata* is efficient in exploiting P from sediments (Barko et al. 1988). On the other hand, James et al. (1996) reported substantial P release from sediments covered by other types of macrophytes (e.g., *Ceratophyllum demersum*, *Elodea canadensis*) and many macrophyte species release P by decomposition (Carpenter 1980). Fortunately, nutrient release in fall from decomposing plants does not influence the predictions of this model, as we focused solely on the summer stratified season, the period in which ecosystem regime shift is most apparent. Macrophyte influence on P recycling may also arise through control of the hydrologic regime of the lake. In general, macrophyte cover is expected to decrease the recycling of P by sediment resuspension (Scheffer 1998). Moreover, sediment resuspension by waves and animals and elimination of macrophytes by winds may also diminish macrophyte effects, especially in shallow lakes. Taken together, this analysis suggests that the effects of macrophytes on P release from sediments are an important uncertainty and should be a priority for future field research.

It is suggested that macrophytes can control algal blooms by providing a refuge for zooplankton against fish (e.g., Scheffer 1998), in addition to their effects on P recycling. We do not know whether this refuge effect produces multiple stable states on its own, but it would reinforce the stability of alternative states triggered by P recycling analyzed here.

Implications for management

We showed that the reversibility of ecosystem regime shift was significantly affected by the physical features of the lake, especially mean depth. Unexpectedly, our analyses also revealed that the most susceptible and least restorable lakes were those with intermediate mean depths (Fig. 2). With respect to eutrophication, such intermediate-depth lakes were too deep to be protected by macrophytes from regime shift, but were also too shallow to mitigate internal P loading through dilution in the hypolimnion. Instead, our findings suggest that such lakes will require stronger restrictions on P loading to reduce the risk of eutrophication and maintain clear water.

The finding that increases in temperature can reduce the critical P loading needed to initiate ecosystem regime shift (e.g., l_1, l_2; Fig. 5C) means that a gradual increase in temperature can cause a regime shift even in a lake where P input is constant, can reduce the domain of ecosystem stability, or can impair the resilience of a clear-water state to disturbance. In contrast, Scheffer et al. (2001*b*) suggested that climate warming may result in recolonization of macrophytes in shallow lakes, which increases the resilience of the clear water state. This recolonization is related to clear-water phases due to zooplankton grazing in spring and the probability of the phases increases with lake temperature (Scheffer et al. 2001*b*). Thus taken together, these analyses suggest that warming may either facilitate or inhibit regime shift, depending on the season in which warming occurs.

Although temperature has not been raised as an important driver of regime shifts in lakes, gradual changes in temperature have been often suggested as one of the key causes for regime shifts in other systems (e.g., desertification in the Sahel region, Zeng et al. 1999). Our study revealed a similar complex interaction of physical, chemical, and biotic processes in regime shifts of lakes. Such multiplicity of causes may be a general feature of regime shifts in ecosystems.

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