Ecology, 93(3), 2012, pp. 619–631

Benthic–planktonic coupling, regime shifts, and whole-lake primary production in shallow lakes

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Abstract. Alternative stable states in shallow lakes are typically characterized by submerged macrophyte (clear-water state) or phytoplankton (turbid state) dominance. However, a clear-water state may occur in eutrophic lakes even when macrophytes are absent. To test whether sediment algae could cause a regime shift in the absence of macrophytes, we developed a model of benthic (periphyton) and planktonic (phytoplankton) primary production using parameters derived from a shallow macrophyte-free lake that shifted from a turbid to a clear-water state following fish removal (biomanipulation). The model includes a negative feedback effect of periphyton on phosphorus (P) release from sediments. This in turn induces a positive feedback between phytoplankton production and P release. Scenarios incorporating a gradient of external P loading rates revealed that (1) periphyton and phytoplankton both contributed substantially to whole-lake production over a broad range of external P loading in a clear-water state; (2) during the clear-water state, the loss of benthic production was gradually replaced by phytoplankton production, leaving whole-lake production largely unchanged; (3) the responses of lakes to biomanipulation and increased external P loading were both dependent on lake morphometry; and (4) the capacity of periphyton to buffer the effects of increased external P loading and maintain a clear-water state was highly sensitive to relationships between light availability at the sediment surface and the of P release. Our model suggests a mechanism for the persistence of alternative states in shallow macrophyte-free lakes and demonstrates that regime shifts may trigger profound changes in ecosystem structure and function.

Key words: eutrophication; lake morphometry; mathematical model; mean depth; periphyton; phosphorus; phytoplankton; regime shift; whole-lake primary production.

Introduction

Ecosystems can undergo rapid state changes that are characterized by a transformation in trophic structure and dynamics. In terrestrial ecosystems, these regime shifts typically involve a sudden transition in dominance between alternative forms of primary producers (Scheffer et al. 2001, Foley et al. 2003). The best described alternative stable states in aquatic ecosystems are also distinguished by different primary producers. Shallow marine systems can shift between coral- and macroalgae-dominated structures and grazers facilitate the persistence of the coral-dominated state (McCook 1999). Shallow lakes can shift between clear macrophyte-dominated states and turbid phytoplankton-dominated states (Moss 1990, Scheffer et al. 1993).

State changes in shallow lakes can manifest as a gradual loss of macrophytes over decadal time scales (Sayer et al. 2010) or occur rapidly and repeatedly over short time scales (Bayley et al. 2007). A third category of state change is the alternative state in which transition between macrophyte and phytoplankton dominance is rapid and often induced by an external forcing factor, but the persistence of each state is reinforced (stabilized) by internal feedback mechanisms (Jeppesen et al. 1990, Moss 1990, Scheffer et al. 1993). Alternative states are characterized by an underlying hysteresis, such that when a regime shift occurs, the system leaves the domain of control of one state and passes through an unstable equilibrium before entering the alternative domain. This requires that positive feedback mechanisms act to accelerate the transition into the alternative state (Scheffer et al. 1993, 2001).

Regime shifts can be used to manage lakes. Biomanipulation of fishes has been used to overcome biological resistance following nutrient loading reduction (Shapiro and Wright 1984, Søndergaard et al. 2008). When zooplanktivorous fish are removed from shallow lakes, the resulting release from predation allows zooplankton to control the phytoplankton biomass. The improved light

Manuscript received 5 November 2010; revised 27 April 2011; accepted 26 August 2011. Corresponding Editor: P. R. Leavitt.

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climate, in turn, facilitates the establishment of macrophytes (Jeppesen et al. 1990). The presence of macrophytes is a clear structural change that differentiates the turbid from the clear-water state (Moss 1990). Macrophytes are thought to be critical for maintaining the clear-water state through a number of mechanisms, including promoting piscivore control of planktivorous fish (Blindow et al. 1993), providing a predation refuge for zooplankton (Burks et al. 2002, Genkai-Kato 2007) and reducing sediment suspension (Barko and James 1998).

The contrasting clear-water and turbid states are functionally different in that benthic primary producers (periphyton and macrophytes) make a substantial contribution to whole-ecosystem production in the clear-water state, while the planktonic primary producer (phytoplankton) overwhelmingly dominates production in the turbid state. Although most studies of stable states in lakes focus on macrophytes and phytoplankton, paleolimnological data demonstrate that the shift from a clear-water to a turbid state also entails a shift in the relative abundance of periphyton and phytoplankton (Anderson et al. 1995, McGowan et al. 2005, Sayer et al. 2010). Experiments and surveys demonstrate that a functional shift from benthic to planktonic dominance of primary production may occur even in the absence of macrophytes. Periphyton is especially important in clear water, such as in lakes and ponds at high latitude or altitude, where periphyton may account for up to 80% of the whole-lake primary production (Brönmark and Hansson 1998). In clear oligotrophic lakes, periphyton on sediments dominates whole-lake primary production, while production is almost entirely restricted to phytoplankton in nutrient-rich lakes (Liboriussen and Jeppesen 2003, Vadeboncoeur et al. 2003). These transitions between algal functional groups have been demonstrated experimentally (Vadeboncoeur et al. 2001) and using models (Vadeboncoeur et al. 2008), but the possibility that under certain circumstances these transitions may represent alternative states has not been explored.

Alternative states have specific diagnostic characteristics including feedback mechanisms that stabilize the current configuration of the ecosystem, a substantial internal resistance to regime shifts, and a clear contrast in ecosystem structure and function between the two states. Due to these stabilizing internal dynamics, the transition to an alternative state is usually generated by stochastic external events such as extreme weather, water level changes, or human manipulation of ecosystems such as fish removal. We postulate that there are conditions where an individual lake could exhibit alternative configurations based on the benthic production (epipelic periphyton on sediments) vs. gplanktonic production (phytoplankton in the water column). First, a lake would have to be relatively small or shallow, such that there is the potential for periphyton to dominate whole-lake primary production (Vadeboncoeur et al. 2008). Second, there would have to be sufficient phosphorus (P), either in the sediments or the biota, such that its liberation would engender a transition to phytoplankton dominance. Thus, we expect regime shifts between periphyton and phytoplankton dominance to be most likely in shallow, polymictic lakes.

Although the above physical criteria set up the potential for either benthic or planktonic dominance of production, a mechanism for stabilizing the alternative states is also required. Periphyton dominance can occur if sufficient light is available at the sediment–water interface to allow the dominance of biofilms. High phytoplankton biomass suppresses periphyton growth by attenuating light. The dependence of water clarity on zooplankton grazing is one potential mechanism for transitions between periphyton and phytoplankton dominance. A second mechanism, whicj is not contingent on food-web configuration, involves the capacity of periphyton to reduce P flux from sediments through uptake and oxygenation (Carlton and Wetzel 1988, Hansson 1989, Van Luijn et al. 1995), and consequently regulate P availability to phytoplankton (Hansson 1990). In this paper, we explore the potential for regime shifts in shallow polymictic lakes based on the dependence of phytoplankton production on the rate of P release from sediments (Søndergaard et al. 1990, 2003) and the concurrent dependence of periphyton production on light availability at the sediment–water interface (Vadeboncoeur et al. 2001, 2003, Karlsson et al. 2009).

Previous models of drivers of periphyton contributions to whole-lake primary production did not include any feedbacks between light, primary production, and internal P loading (Vadeboncoeur et al. 2008). In contrast, a model exploring the effects of macrophytes on sediment P release demonstrated that macrophytes can generate a state change from turbid to clear water assuming (1) the presence of macrophytes prevented any P release and (2) the absence of macrophytes allowed maximum P release from sediments (Genkai-Kato and Carpenter 2005). The assumption of a threshold-like response of P release to the presence or absence of macrophytes is not unambiguously supported by field data and experiments (Perrow et al. 1994, Stephen et al. 1997). It is more likely that the realized rate of P release from sediments varies smoothly as a function of the degree of oxygenation of the sediments by periphyton and macrophytes and the rate of deoxygenation of the sediments at night (Frodge et al. 1991). High benthic respiration rates can cause sediment hypoxia and anoxia even when mixing maintains the water column in an oxygen-saturated state in eutrophic shallow lakes (e.g., Søndergaard et al. 1990). Here we explore the sensitivity of the relative distribution of benthic and planktonic primary production to internal controls on P release from sediments using a simple dynamics model based on empirical data. To parameterize the model, we use data from Lake Engelsholm, a Danish lake in which epipelic periphyton is the dominant benthic primary producer. Lake Engelsholm was successfully shifted from a turbid to a clear-water state by biomanipulation (Søndergaard

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

Symbol	Meaning	Units	Value	Source
State variables				
A	phytoplankton density	mg chl/m^3		
P	phosphorus concentration	mg P/m^3		
z	depth	m		
Functions				
F	photosynthetic rate of periphyton	mg C·m^{-2}·h^{-1}		Eq. 9
I	underwater light intensity	μmol·m^{-2}·s^{-1}		Eq. 5
R	areal P release rate	mg P·m^{-2}·d^{-1}		Eq. 6
S	proportion of lake area shallower than depth z	dimensionless		Eq. 3
BP	whole-lake primary production of periphyton	kg C/h		Eq. 10
PP	whole-lake primary production of phytoplankton	kg C/h		Eq. 8
Parameters				
a	critical relative underwater light intensity parameter	dimensionless	0.13	1
e	release of ingested P by zooplankton	dimensionless	0.4	2, 3
$F_{\max}$	maximum photosynthetic rate of periphyton	mg C·m^{-2}·h^{-1}	76.5	4
g	zooplankton grazing rate	d^{-1}	0.13, 0.22†	1, 5
h	flushing rate	d^{-1}	0.0127	1
I_0	light intensity at water surface	μmol·m^{-2}·s^{-1}	600	6
I_k	light intensity at onset of saturation	μmol·m^{-2}·s^{-1}	130	7
k	half-saturation constant for phytoplankton growth rate	mg P/m^3	4.5	8
L	areal external P loading rate	mg P·m^{-2}·d^{-1}	2.664	1
l	volumetric external P loading rate	mg P·m^{-3}·d^{-1}	$= L/\bar{z}$	
q	phytoplankton P content	mg P/mg chl	0.15	1
$\bar{R}$	mean areal P release rate	mg P·m^{-2}·d^{-1}		Eq. 7
R_0	maximum areal P release rate	mg P·m^{-2}·d^{-1}	10.83	1
r	volumetric P release rate	mg P·m^{-3}·d^{-1}	$= \bar{R}/\bar{z}$	
s	phytoplankton shading attenuation coefficient	m^2/mg chl	0.021	1
s_0	background light attenuation coefficient	m^{-1}	0.5	1
V	lake volume	m^3		
v	phytoplankton sinking rate	m/d	0.25	6
$\bar{z}$	mean depth	m		
z_{m}	maximum depth	m		
γ	curvature coefficient for R–I relationships	dimensionless	0.767	1
θ	C:chl ratio of phytoplankton	mg C/mg chl	30	5
μ	maximum growth rate of phytoplankton	d^{-1}	0.76	8

Notes: The source column shows the references for parameter values or for data to which the model was fit for estimating parameter values. Sources are coded as follows: 1, Lake Engelsholm data; 2, Carpenter (1992); 3, Grover (1995); 4, Liboriussen and Jeppesen (2003); 5, Jeppesen et al. (1994); 6, Diehl (2002); 7, Nozaki (2001); 8, Sommer (1989).

† Value after the biomanipulation effect.

et al. 2002). The transition occurred without the establishment of submerged macrophytes, suggesting that other mechanisms maintained the clear-water state.

THE MODEL

The basic model is composed of two dynamic variables that characterize water column trophic status, phytoplankton density (A) and phosphorus (P) concentration:

$$\frac{dA}{dt} = \frac{\mu P}{k+P}A - \left(g + \frac{v}{\bar{z}} + h\right)A \qquad (1)$$

$$\frac{dP}{dt} = l + r + qegA - \frac{q\mu P}{k+P}A - hP. \qquad (2)$$

The meanings and units of the variables and parameters are listed in Table 1.

Growth of phytoplankton is described by the Monod function (Tilman 1982). Phytoplankton loss occurs through grazing by zooplankton, sinking, and flushing from the lake. Inputs of dissolved P into the water column derive from external loading from the watershed, internal loading (release from sediments), and excretion of P when phytoplankton is grazed by zooplankton. Loss of P from the dissolved pool occurs via sequestration in phytoplankton and flushing from the lake.

Lake morphometry

Lake basins are modeled by quadric surfaces, following the approach by Genkai-Kato and Carpenter (2005). The proportion of the lake's surface area that encompasses water depth shallower than z is given by

$$S(z) = 3\left(2\frac{\bar{z}}{z_{\mathrm{m}}} - 1\right)\left(\frac{z}{z_{\mathrm{m}}}\right)^2 - 2\left(3\frac{\bar{z}}{z_{\mathrm{m}}} - 2\right)\frac{z}{z_{\mathrm{m}}} \qquad (3)$$

where $\bar{z}$ and z_{m} are the mean and maximum depths of the lake, respectively (Carpenter 1983). The proportion of the lake's area between depths z and $z + dz$ is calculated as

$$\Delta S = S(z+dz) - S(z) = \left[\frac{6(2D-1)}{z_{\mathrm{m}}^2}z - \frac{2(3D-2)}{z_{\mathrm{m}}}\right]dz \qquad (4)$$

where D is the depth ratio ($D = \bar{z}/z_{\mathrm{m}}$) and dz is an incremental change in depth.

P release from sediments

The rate of P release from sediments is mediated by the photosynthetic activity of periphyton on the sediments (Carlton and Wetzel 1988, Hansson 1989). Because sediments are rich in nutrients (Kalff 2002), the photosynthetic activity of periphyton depends on the light intensity at sediment surfaces (Vadeboncoeur et al. 2001). We modeled light intensity at depth z using the Lambert–Beer law:

$$I(z,A) = I_0 \ \exp[-(s_0 + sA)z] \tag{5}$$

where I_0 is the incident light intensity at the water surface, s_0 is the phytoplankton-independent background light attenuation coefficient, s_1 is the specific light attenuation coefficient per unit of phytoplankton biomass, and A is the phytoplankton density (Kirk 1994, Vadeboncoeur et al. 2008). The areal P release rate from the sediment at depth z, $R(z)$, is assumed to be negatively related to light intensity:

$$R(z) = \begin{cases} R_0\left[1 - \left(\dfrac{I(z)}{aI_0}\right)^{\gamma}\right] & \text{for } I(z) \le aI_0 \\[2ex] 0 & \text{for } I(z) > aI_0. \end{cases} \tag{6}$$

The parameter a is the proportion of incident light below which P release from the sediment occurs. Release of P is initiated ($R(z) > 0$) when the relative light availability at depth z is darker than a (i.e., $I(z)/I_0 < a$). Phosphorus release is maximal (R_0) when no light is available at the sediment–water interface ($I(z) = 0$). The absence of light precludes sediment oxygenation by periphyton. Rather than assume a threshold response of periphyton to light intensity (Genkai-Kato and Carpenter 2005), we use the exponent γ to describe the relationship between P release ($R(z)$) and light availability. Because light availability on sediments depends on trophic status, γ is a parameter that links the P release rate to trophic status. The relationship between $R(z)$ and $I(z)$ is negative. The shape of the relationship is linear when $\gamma = 1$, concave when $\gamma > 1$, and convex when $\gamma < 1$.

The areal P release from the sediment, encompassing the water depth between z and $z + dz$, is given by $R(z)\Delta S$. The average areal P release rate in the whole lake is

$$\begin{aligned} \bar{R} &= \int_0^{z_{\mathrm{m}}} R(z)\Delta S \\ &= R_0 \int_0^{z_{\mathrm{m}}} \left\{1 - \frac{\exp[-\gamma(s_0 + sA)z]}{a^{\gamma}}\right\}(\alpha z - \beta)dz \\ &= R_0\left(\frac{\alpha z_{\mathrm{m}}^2}{2} - \beta z_{\mathrm{m}}\right) \\ &\quad + \frac{\alpha R_0}{a^{\gamma}}\left[\frac{z_{\mathrm{m}} e^{-\gamma(s_0+sA)z_{\mathrm{m}}}}{\gamma(s_0 + sA)} - \frac{1 - e^{-\gamma(s_0+sA)z_{\mathrm{m}}}}{\gamma^2(s_0 + sA)^2}\right] \\ &\quad + \frac{\beta R_0}{a^{\gamma}}\frac{1 - e^{-\gamma(s_0+sA)z_{\mathrm{m}}}}{\gamma(s_0 + sA)} \end{aligned} \tag{7}$$

where $\alpha = 6(2D - 1)/z_{\mathrm{m}}^2$ and $\beta = 2(3D - 2)/z_{\mathrm{m}}$. The volumetric P release rate averaged over the whole lake is given by $r = \bar{R}/\bar{z}$.

Benthic vs. planktonic primary production

Whole-lake production is calculated by summation of productivity by phytoplankton (PP, kg C/h) and by periphyton (BP, kg C/h). We assume that the growth of phytoplankton is limited by P and that of periphyton by light. Primary productivity of phytoplankton is calculated based on the P-dependent dynamics of phytoplankton density (Eq. 1), using the following formula:

$$\mathrm{PP} = \frac{\theta V}{24}\frac{\mu P}{k + P}A \tag{8}$$

where θ and V are the carbon : chlorophyll ratio of phytoplankton and volume of the lake, respectively. The lake volume is given by the mean depth multiplied by lake area. We assume that the water is well mixed, so that the entire phytoplankton community is affected by the collective consumption of nutrients and light throughout the water column.

The productivity of periphyton is dependent upon the prevailing light conditions at the sediment–water interface. The photosynthetic rate (F, mg $\mathrm{C{\cdot}m^{-2}{\cdot}h^{-1}}$) is a function of light intensity (I) at depth z using the photosynthesis–irradiance response curve of Tamiya (1951):

$$F(I) = F_{\max}\frac{I(z)/I_{\mathrm{k}}}{1 + I(z)/I_{\mathrm{k}}} \tag{9}$$

where $F_{\max}$ is the maximum photosynthetic rate and I_{k} is light intensity at the onset of light saturation (intersection of $F_{\max}$ and initial slope of the photosynthesis–irradiance curve). We use averaged values of 76.5 mg $\mathrm{C{\cdot}m^{-2}{\cdot}h^{-1}}$ for $F_{\max}$ (Liboriussen and Jeppesen 2003) and 130 $\mu\mathrm{mol{\cdot}m^{-2}{\cdot}s^{-1}}$ for I_{k} (Nozaki 2001). The whole-lake production of periphyton is calculated by

$$\mathrm{BP} = \int_0^{z_{\mathrm{m}}} F(I)\Delta S \tag{10}$$

where $F(I)$ is the photosynthetic rate of periphyton at a given depth (Eq. 9) and ΔS is the surface area of the sediments for each depth interval (Eq. 4).

Parameterization and sensitivity analyses

Values of parameters are estimated based on data for the summer season collected for the years 1989–2004 from Lake Engelsholm, Denmark (area 0.44 km^2, maximum depth 6.1 m, mean depth 2.6 m). Planktivorous fish were removed from the lake in 1992 (11.5 Mg), 1994 (6.8 Mg), and 1996 (3.9 Mg). Marked contrasts were evident for numerous lake characteristics before and after the biomanipulation (Søndergaard et al. 2008). For instance, the mean summer chlorophyll *a* concentration decreased (98 ± 23.7 [mean ± SD] $\mathrm{mg/m^3}$ in 1989–1993, 41.4 ± 10.3 in 1994–2004) and the zooplankton grazing rate increased (0.13 ± 0.03 d^{-1} in 1989–1993, 0.22 ± 0.06 in 1994–2004, estimations based on Jeppesen et al. [1994]). Data in 1998 contain low chlorophyll concentration and extremely high estimated grazing rate and are not included in our analyses.

Parameters other than a, q, R_0, and γ are difficult to estimate from Lake Engelsholm data and are obtained from the literature (Table 1). The parameters for a, q, R_0, and γ in Eqs. 2 and 6 were numerically estimated by fitting the model to summer chlorophyll a concentrations in Lake Engelsholm in 1989–2004. The critical light intensity at which P begins to be released from sediments (a) is estimated by changing its value between 0.003 ($\sim$1.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$, corresponding to the compensation irradiance of ice algae [Kühl et al. 2001]) and 0.17 ($\sim$100 $\mu mol \cdot m^{-2} \cdot s^{-1}$) with increments of 0.001 when $a \leq 0.01$ and 0.005 when $a > 0.01$. We vary the P content of phytoplankton (q) between 0.15 and 0.82 with increments of 0.01, based on the mean value and standard deviation (SD) of 307 and 212, respectively, for the C:P ratio in freshwater systems (Elser et al. 2000) and a phytoplankton C : chlorophyll ratio of 30 (Jeppesen et al. 1994). Littoral sediments release P even if the water above the sediments is oxic (Carlton and Wetzel 1988, Søndergaard et al. 1990, Caraco et al. 1992), but the realized rate of release ($\bar{R}$) depends on oxygen concentrations immediately below the sediment–water interface. In lakes, the maximum potential release rate (R_0) under anoxic conditions depends on the magnitude of the sediment P pool and temperature. We solve for R_0 in Lake Engelsholm by iteratively varying R_0 between 0 and 21 mg $P \cdot m^{-2} \cdot d^{-1}$ with increments of 0.5, where 21 is the mean + SD value reported for anoxic, P-rich lake sediments (Nürnberg 1984). In the model, we allow periphyton to mitigate P release rates through oxygen evolution. Parameter γ determines the shape of the relationship between P release from sediments and light. We vary γ between 0.1 and 10 with increments of 0.01 when $\gamma \leq 1$ and 0.1 when $\gamma > 1$, covering concave and convex curves. We estimate the values of a, q, R_0, and γ for Lake Engelsholm before and after biomanipulation by iteratively changing their values in the model and searching for parameter sets that result in chlorophyll a concentrations close to the observed data in each year. We then average the top three parameter sets that best fit the observed data to obtain estimates of a, q, R_0, and γ.

Sensitivity analyses are performed by calculating the changes in whole-lake production and the periphyton contribution to whole-lake production across an external P loading gradient in response to changes in the value of a, q, R_0, and γ. We also explore the sensitivity of the model to variation in the maximum photosynthetic rate of periphyton (F_{max}), background light attenuation (s_0), and phytoplankton shading attenuation (s). Parameters a, q, R_0, and γ are varied over the same ranges as their parameter estimation. F_{max} is varied between 5 and 120 mg $C \cdot m^{-2} \cdot h^{-1}$ (Vadeboncoeur et al. 2008), s_0 between 0.08 and 2 m^{-1} (Kirk 1994), and s between 0.007 and 0.066 m^2/mg chl (Dubinsky and Berman 1979, Reinart et al. 2003).

We explore the effects of morphometry on the expression of stable states by continuously varying both depth ratio (0.34–0.67) and mean depth (1.6–3.6 m). We further explore the effect of morphometry on periphyton and phytoplankton contributions to whole-lake primary production by increasing or decreasing the mean depth of Lake Engelsholm by 1 m.

RESULTS

The ranges of the three parameter sets that best fit the Lake Engelsholm data were as follows: a, 0.11–0.155; q, 0.15 mg P/mg chl a (no variation); R_0, 10.5–11.0 mg $P \cdot m^{-2} \cdot d^{-1}$; and γ, 0.63–0.93. We averaged these to obtain the parameter set $(a, q, R_0, \gamma) = (0.13, 0.15, 10.83, 0.767)$. There was good agreement between the model and the observed chlorophyll concentrations in the turbid state before biomanipulation (1989–1993; Fig. 1A). However, the model produced slightly lower chlorophyll concentrations than those observed in Lake Engelsholm in the clear-water state after biomanipulation (Fig. 1A). In the model, the clear-water state was characterized by a virtual cessation of P release from sediments (Fig. 1B). The alternative (turbid and clear-water) states can be visualized by overlaying plots of the straight line for P loss processes (sinks) and the curve for P sources (Fig. 1C, D). Under low grazing rates before biomanipulation, the curve intersected at three points (Fig. 1C). The central point was a repeller (unstable equilibrium) that lay between two stability domains. The lower and upper intersections were attractors (stable equilibria), one for the clear-water state and the other for the turbid state. When grazing by zooplankton increased after biomanipulation ($g = 0.13 \rightarrow 0.22$), the curve had a single intersection (clear-water state, Fig. 1D).

Our sensitivity analyses demonstrated that the presence or absence of a regime shift by increased external P loading depended upon parameters a, q, R_0, γ, s_0, and s (Fig. 2). The value of R_0 affected the magnitude of the difference between whole-lake production before and after a regime shift (Fig. 2C). Weak photosynthetic potential of periphyton resulted in a low benthic contribution before a regime shift (Fig. 2E). The sensitivity analyses indicated that whole-lake production before a regime shift could decrease slightly with increased external P loading when the maximum photosynthetic rate of periphyton was high ($F_{max} = 120$, Fig. 2E), background light attenuation small ($s_0 = 0.08$, Fig. 2F) or the phytoplankton shading attenuation coefficient large ($s = 0.066$, Fig. 2G).

Our morphometrical analyses showed that the response of lakes to biomanipulation depended on mean depth and depth ratio (Fig. 3). Lakes with low depth ratios exhibited the potential for restoration over a broader range of mean depths than did lakes with higher depth ratios (Fig. 3). The response of lakes to increased

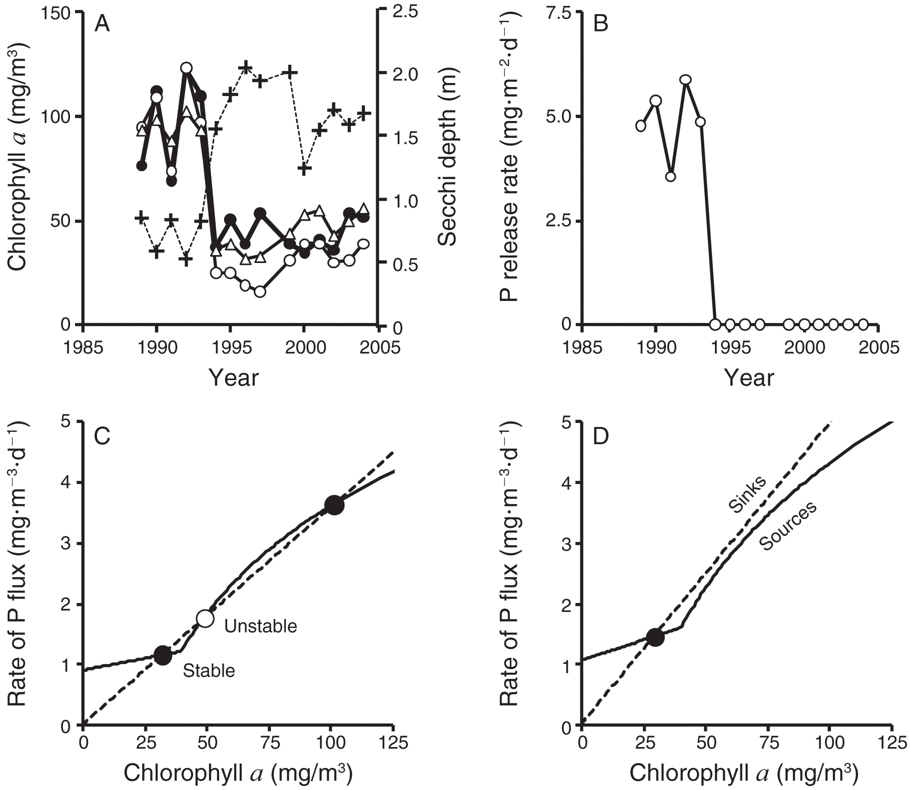

FIG. 1. (A) Observations (solid circles) and predictions (open circles) from the model with estimated parameters for changes in mean chlorophyll *a* concentration and observed Secchi depth (crosses) in the summer season in Lake Engelsholm, Denmark, during 1989–2004. Chlorophyll *a* concentrations predicted from the light-independent model where P release is uncoupled from photosynthetic activity of periphyton are also plotted (open triangles). (B) Mean areal P release rates from sediments ($\bar{R}$) during 1989–2004 predicted from the model. (C, D) Rates of P flux vs. chlorophyll *a* concentration (C) before and (D) after biomanipulation, according to Eq. 2. The solid lines represent the P sources (external and internal loading). The broken lines are the rate of P loss. Intersections of these lines are equilibria. The solid and open circles denote the stable and unstable equilibria, respectively. The parameters for grazing (g), flushing (h), and external P loading (L) rates are the averaged values before and after biomanipulation in Lake Engelsholm: (C) $g = 0.13$ d^{-1}, $h = 0.0117$ d^{-1}, $L = 2.36$ mg P·m^{-2}·d^{-1}; (D) $g = 0.22$ d^{-1}, $h = 0.0131$ d^{-1}, $L = 2.8$ mg P·m^{-2}·d^{-1}.

external P loading depended on mean depth (Fig. 4). Lakes at the shallower end of the analysis range exhibited regime shifts at higher external P loading than deeper lakes (Fig. 4A). Phytoplankton densities in the clear-water and turbid states decreased as a function of mean depth (Fig. 4B). The potential for a regime shift was not dependent on lake area, because the proportion of area shallower than a given depth was independent of the lake's surface area (Eq. 3).

We modeled the effects of increasing and decreasing the mean depth of Lake Engelsholm (area 0.44 km^2, depth ratio 0.426) by 1 m to explore the effects of lake morphometry on the distribution of whole-lake primary production. During the clear-water state, whole-lake primary production gradually increased with external P loading when Lake Engelsholm's depth was decreased by 1 m (Fig. 5A). In contrast, when mean depth was increased by 1 m, increases in phytoplankton production compensated for declines in periphyton production, leading to little or no overall increase in whole-lake primary production (Fig. 5B, C). The proportion of periphyton contribution to whole-lake production declined with external P loading in all lakes. Periphyton and phytoplankton both made substantial contributions to whole-lake production over a broader range of external P loading levels, and the decline in periphyton contribution following a regime shift was smaller, in shallow lakes compared with deep lakes (Fig. 5).

DISCUSSION

Our model used empirical data from Lake Engelsholm to explore feedbacks between phytoplankton production, light, periphyton production, and P release from sediments. Using pre- and post-biomanipulation data from this shallow lake, we found that variation in light could indirectly lead to positive feedbacks between phytoplankton density and P release from sediments. The model exhibited regime shifts in which primary production was dominated by either periphyton (clear-water phase) or phytoplankton (turbid phase). This result is similar to both theoretical and empirical studies that demonstrate that littoral macrophytes can cause

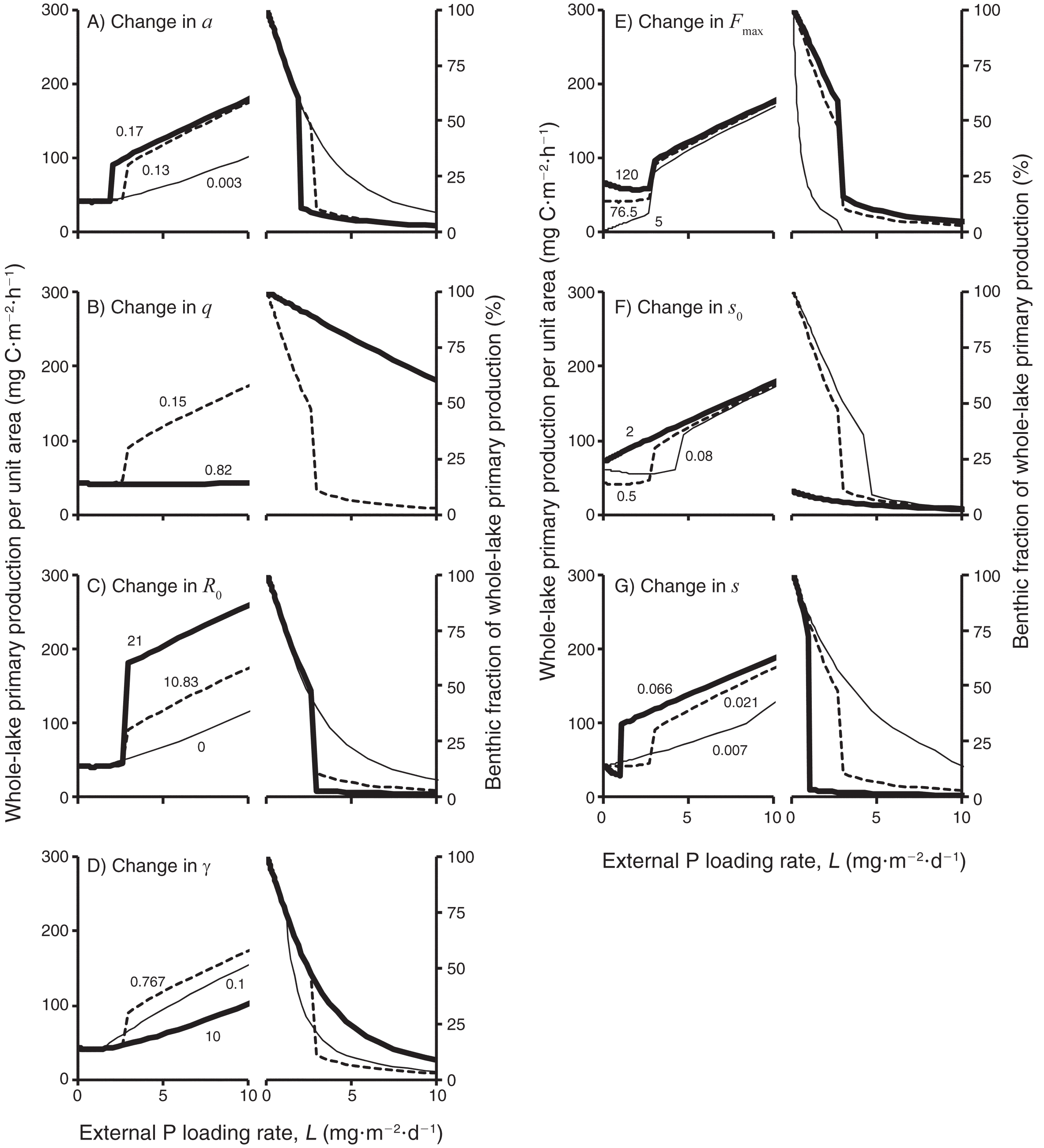

FIG. 2. Effects of a change in one parameter on whole-lake primary production (left side of each panel) and relative contribution of periphyton to whole-lake production (right side of each panel) in Lake Engelsholm (area 0.44 km^2, mean depth 2.6 m). The changed parameter is (A) critical relative underwater light intensity, a (thin line, $a = 0.003$; broken line, $a = 0.13$; thick line, $a = 0.17$), (B) phytoplankton P content, q (broken line, $q = 0.15$; thick line, $q = 0.82$), (C) maximum areal P release rate, R_0 (thin line, $R_0 = 0$; broken line, $R_0 = 10.83$; thick line, $R_0 = 21$), (D) curvature coefficient for the relationship of underwater light intensity and areal P release rate (I–R relationships, γ) (thin line, $\gamma = 0.1$; broken line, $\gamma = 0.767$; thick line, $\gamma = 10$), (E) maximum photosynthetic rate of periphyton, F_{max} (thin line, $F_{max} = 5$; broken line, $F_{max} = 76.5$; thick line, $F_{max} = 120$), (F) background light attenuation coefficient, s_0 (thin line, $s_0 = 0.08$; broken line, $s_0 = 0.5$; thick line, $s_0 = 2$), (G) phytoplankton shading attenuation coefficient, s (thin line, $s = 0.007$; broken line, $s = 0.021$; thick line, $s = 0.066$). Note that the broken lines correspond to the original parameter values used in our numerical analyses.

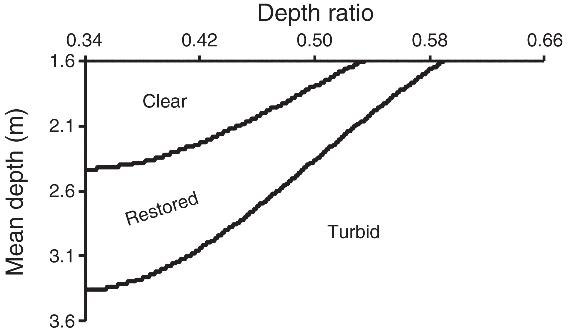

FIG. 3. Effects of biomanipulation in which the grazing rate is changed from 0.13 to 0.22 d^{-1} on water clarity in relation to mean depth and depth ratio. Depth ratio is the ratio of mean depth to maximum depth. In the region of the graph labeled "clear," a lake has a single clear-water state even before biomanipulation; in the "restored" region, lakes shift from a turbid state to a single clear-water state due to biomanipulation; in the "turbid" region, lakes remain persistently turbid in spite of biomanipulation.

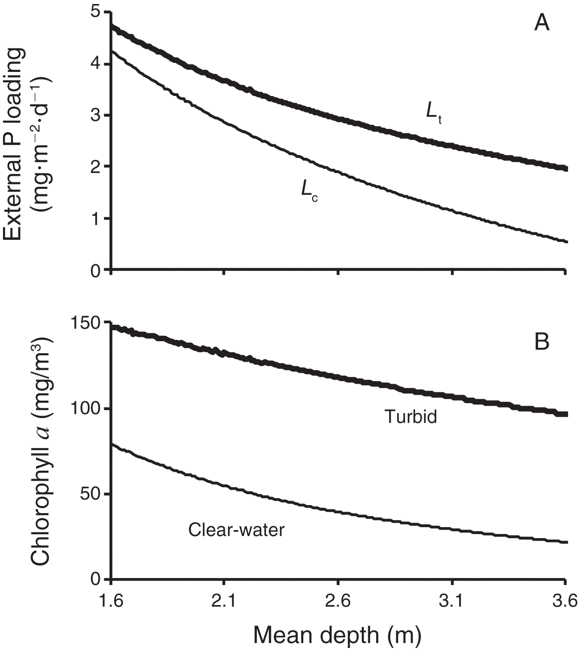

FIG. 4. Response of lakes to increased external P loading in relation to mean depth. Parameters are all based on data from Lake Engelsholm prior to biomanipulation except for mean depth. (A) The equilibrium state of a lake is classified into three patterns according to the external P loading rate (L). The lake is in a clear-water state below a critical value of P loading (L_c, thin line). A regime shift from a clear-water state to a turbid state occurs when P loading exceeds a critical value for turbidity (L_t, thick line). The lake has potentially three equilibria with regard to phytoplankton density when $L_c < L < L_t$. (B) Phytoplankton densities (mg chl/m^3) before (clear-water state, thin line) and after (turbid state, thick line) a regime shift when L exceeds L_t.

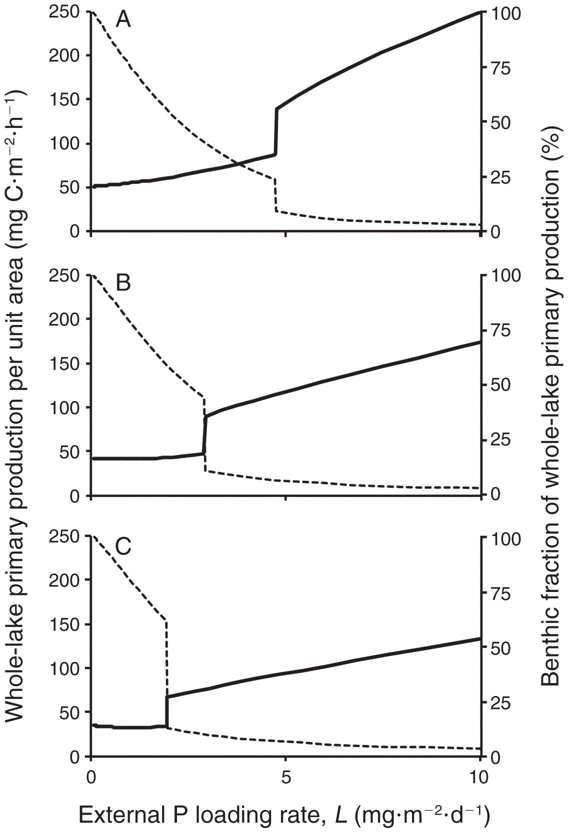

FIG. 5. Effects of increased external P loading on whole-lake primary production (solid line) and relative contribution of periphyton to whole-lake production (broken line) in relation to mean depth. Based on the morphometry of Lake Engelsholm (area 0.44 km^2, mean depth 2.6 m), its mean depth is (A) decreased (1.6 m), (B) unchanged (2.6 m), or (C) increased (3.6 m).

regime shifts in lakes (Jeppesen et al. 1990, Moss 1990, Scheffer et al. 1993, Genkai-Kato and Carpenter 2005, Genkai-Kato 2007). However, the mechanism generating regime shifts in our analysis is regulation of P release by periphyton rather than the myriad of structural effects generated by macrophytes.

The crucial mechanism underlying the regime shift was the ability of periphyton to regulate P release from sediments, through direct uptake, oxidation of the sediment–water boundary layer, or both (Carlton and Wetzel 1988, Van Luijn et al. 1995). Parameterization of the light-dependent model using Lake Engelsholm data indicated that sediment P release was effectively zero when light intensity at the sediment–water interface was greater than 13% ($a = 0.13$) of the surface light intensity, corresponding to 78 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The effect of periphyton on P release and light condition is largely unquantified, but Carlton and Wetzel (1988) and Van Luijn et al. (1995) experimentally showed that periphyton inhibited P release from sediments at illuminations of 30 and 85 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. The value of 78

μmol·m^{-2}·s^{-1} falls within this range, but we emphasize that this is a rate estimated from empirical data from Lake Engelsholm. As such, the value reflects average sediment P release rates over a 24-h cycle. Carlton and Wetzel (1988) found that P release was near 0 during illumination at 30 μmol·m^{-2}·s^{-1}, but rapidly increased upon onset of darkness. Thus, it is possible that the light intensity at which P release from sediments is inhibited in Lake Engelsholm is substantially lower than 78 μmol·m^{-2}·s^{-1}, but that P release rates accelerate during darkness.

The value of the critical light intensity, a, determined whether a lake exhibits a smooth transition from periphyton to phytoplankton dominance or exhibits alternative states (Fig. 2A). The critical light intensity also strongly influenced the realized phytoplankton density at a given external P loading. The sensitivity of P release from sediments, and subsequently phytoplankton biomass, to the value of a underscores the strong need for a thorough empirical investigation of the effect of light intensity on sediment P release rates from littoral sediments.

The maximum P release rate from sediments under the no-light condition estimated from a polymictic oxic lake ($R_0 = 10.83$) was lower than the mean value for anoxic sediments (14) reported by Nürnberg (1984). The rate of P release from oxic sediments is generally lower than that from anoxic sediments (Nürnberg 1984). However, considerable amounts of P can be released even from aerobic sediments in shallow Danish lakes in the summer season (Jensen and Andersen 1992). Temperature is also an important determinant of P release and rates of P release from sediments are high in summer (Jensen and Andersen 1992). Despite the potential for higher P release rates in summer, the P release in clear-water lakes is small, and this is likely due to periphyton production (Jeppesen et al. 2005).

Previous simple models have either failed to incorporate P release into models of whole-lake production (Vadeboncoeur et al. 2008), or have set sediment P release to either 0 in the presence of macrophytes or the maximum rate in their absence (Genkai-Kato and Carpenter 2005). In the current model, we allowed P release from sediments to vary as a function of light between the maximum rate R_0 when no light reached the sediments and 0 at the critical light intensity (a). Using the Lake Engelsholm data, the shape parameter of this function, γ value, took a value slightly smaller than 1, indicating that the rate of P release from sediments decreased with irradiance in a nearly linear manner. Data on the value of γ are not readily available, but Havens et al. (2001) showed that the quantity of P bound in periphyton increased with irradiance in a linear, but slightly saturating, manner. Thus, it is possible that the shape of the variation in P release represents variation in direct uptake of P by periphyton or variation in periphyton biomass. However, periphyton also affects sediment pH and redox state, both of which influence P movement across the sediment–water interface (Carlton and Wetzel 1988, Søndergaard et al. 2003).

Our sensitivity analyses showed that periphyton and phytoplankton both contribute substantially to whole-lake primary production in lakes over a broad range of P loading when (1) periphyton strongly suppressed P release from sediments at low light levels (smaller a, Fig. 2A), (2) phytoplankton P content was high (larger q, Fig. 2B), (3) maximum P release rate was low (smaller R_0, Fig. 2C), (4) R–I relationship was concave (larger γ, Fig. 2D), and (5) competitive influence of phytoplankton on periphyton for light was small (smaller s, Fig. 2G). Parameters a, γ, and s are related to the photosynthetic ability of periphyton, which is largely unknown. It has been experimentally shown that the rate of P release from sediments is inversely related to the magnitude of periphyton photosynthesis (Carlton and Wetzel 1988), but there is virtually no information on how this relationship varies across lake ecosystems. There is somewhat more information on phytoplankton P content, which ranges over an order of magnitude and is dependent on species composition (Duarte 1992).

The simulations indicated that the responses of lakes to biomanipulation and increased external P loading were both functions of mean depth (Figs. 3 and 4). It is noteworthy that the loss of benthic production was almost fully compensated by an increase in planktonic production, except for very shallow lakes (Fig. 5). This compensation is consistent with previous findings in North American and European shallow lakes (Vadeboncoeur et al. 2001, 2003, Liboriussen and Jeppesen 2003). However, our sensitivity analyses also indicated that there were conditions under which whole-lake primary production counter-intuitively may decrease with increased external P loading. The decrease in whole-lake production occurred when the maximum photosynthetic rate of periphyton ($F_{\max}$) or phytoplankton shading attenuation coefficient (s) was large (Fig. 2E, G). Liboriussen and Jeppesen (2003) reported $F_{\max}$ values as high as 285 mg C·m^{-2}·h^{-1} in summer in a Danish lake. Although typical values for s fall within the range of 0.007–0.029 (Kirk 1994), a value of 0.23 has also been reported by Megard and Berman (1989) in the Mediterranean Sea. A decrease in whole-lake primary production across a phosphorus gradient due to reductions of light availability to highly productive periphyton has been demonstrated in high latitude Swedish lakes (Karlsson et al. 2009).

Our model does not include all mechanisms involved in benthic-planktonic production and coupling. It is unlikely that P release from sediments can be completely eliminated by periphyton in nutrient rich lakes. Respiration combined with no benthic primary production at night may result in P release mediated by low O_2, despite high uptake in the daytime. These daily dynamics as well as any temperature effects were only indirectly incorporated into the model through parameterization based on empirical data from Lake Engelsholm. Our model does not address the effect of periphyton on sediment resuspension. Periphyton tends to stabilize unconsolidated littoral sediments, increasing the resistance to wind-driven resuspension events (Neumeier et al. 2006). The capacity for periphyton to stabilize sediments would act to reinforce the negative feedback between periphyton production and sediment P release that was already built into the model. We further emphasize that this model should be used with caution outside the depth range we have discussed here (1.6–3.6 m). Other mechanisms such as sediment resuspension become critical in very shallow lakes, while in deeper lakes, stratification alters internal P loading dynamics.

Sediment resuspension by fish is also an important mechanism affecting P release in shallow lakes (Søndergaard et al. 2003) and biomanipulation may have substantially reduced bioturbation by fish in Lake Engelsholm. In addition to the light-dependent model of P release (Eqs. 5–7), we here briefly consider a light-independent model where P release is uncoupled from the photosynthesis rate of periphyton to see effects of bioturbation. In the light-independent scenario, the rate of P release (r) is a constant independent of phytoplankton shading (i.e., $r = r_{\mathrm{const}}$). Setting the right-hand side of Eq. 2 to zero, we have $r_{\mathrm{const}} = q[\mu P/(k+P) - eg]A + hP - l$. Applying the observed data $A = 98$ and $g = 0.13$ before and $A = 41.4$ and $g = 0.22$ after biomanipulation in Lake Engelsholm to the equation, we can obtain the volumetric P release rate: $r_{\mathrm{const}} = 1.75$ (areal rate: 4.56 mg $\mathrm{P{\cdot}m^{-2}{\cdot}d^{-1}}$), before and 0.52 (1.35 mg $\mathrm{P{\cdot}m^{-2}{\cdot}d^{-1}}$) after biomanipulation. The light-independent model produces chlorophyll concentration less precisely before biomanipulation than the light-dependent model, whereas there is better agreement between the alternative model and observed chlorophyll data after biomanipulation (see Fig. 1A). Although both models include the effects of periphyton and fish, the light-dependent case directly examines the effect of photosynthetic activity of periphyton while the light-independent version simply describes the overall effect of fish removal on P release. This comparison between the light-dependent and light-independent models suggests that the light condition for photosynthetic activity of periphyton is the paramount control affecting P release in the turbid (i.e., low-light) state. In contrast, the light-independent model fits the post-biomanipulation data better (Fig. 1A), and predicts that P release occurs at a rate of 1.35 mg $\mathrm{P{\cdot}m^{-2}{\cdot}d^{-1}}$ after biomanipulation. Previously estimated P release rates in the summer season of Lake Engelsholm of 6 and 2 mg $\mathrm{P{\cdot}m^{-2}{\cdot}d^{-1}}$ before and after biomanipulation, respectively (Søndergaard et al. 2002), are comparable to the predicted release rates in our study. There are a variety of possible explanations for the continued release of low levels of P after biomanipulation including an enhanced abundance of invertebrate grazers due to release from fish predation (Jones and Sayer 2003).

We deliberately did not include submerged macrophytes and their associated epiphytes in the model. Other models have explored the effects of submerged macrophytes on water clarity and whole-lake production (Scheffer et al. 1993, Genkai-Kato and Carpenter 2005), but a major goal of our analyses was to assess mechanisms for alternative states in the absence of macrophytes. Macrophytes sometimes fail to reestablish in biomanipulated lakes due to grazing by herbivorous waterfowl, a lack of propagules or poor sediment quality (Lauridsen et al. 2003). Further, prolonged periods of a sustained clear-water state in the absence of macrophytes have been demonstrated in several shallow lakes, including Lake Engelsholm (Jeppesen et al. 2005). Our analyses provide a plausible internal mechanism for these successes: positive feedbacks between periphyton and P release from sediments can reinforce the alternative states in shallow, polymictic lakes. The model suggests that manipulations that improve water clarity (such as planktivorous fish removal) would have highest impact on internal P loading through enhanced photosynthetic activity of periphyton and reduced sediment resuspension by fish in shallow lakes.

Unraveling the mechanisms for alternative states is difficult in spatially extensive ecosystems, and demonstration of alternative states requires a combination of approaches. Our analyses were based on experimental observation (biomanipulation), consideration of ecosystem scales (lake morphometry), and a realistic reaction of P release from sediments as a function of light availability for periphyton. Our model, which can plausibly explain field data, demonstrated that feedbacks between periphyton, phytoplankton and light availability theoretically can generate alternative states in shallow lakes. We lacked the data to disentangle the relative effects of fish bioturbation, grazing invertebrates, and oxygenation by periphyton on sediment P release. The better fit of the light-independent model after biomanipulation (Fig. 1A) suggests that even under optimal light conditions, periphyton did not completely eliminate P release from the sediments in a lake with extremely high sediment P storage such as Lake Engelsholm. We argue that in the absence of macrophytes, periphyton may form an alternative state to phytoplankton dominance in shallow lakes.

At present, it is difficult to assess how common periphyton-dominated clear lakes are relative to those in which macrophytes dominate the clear-water state. Periphyton dominance in the absence of macrophytes is well known from nutrient-poor lakes and lakes with low conductivity (Björk-Ramberg and Ånell 1985, Hecky and Hesslein 1995, Vadeboncoeur et al. 2001, 2003, Bonilla et al. 2005). However, dominance of primary production by periphyton has also been observed in more nutrient-rich, non-manipulated lakes in which macrophytes are scarce or absent (Liboriussen and Jeppesen 2003, Vander Zanden et al. 2006; E. Jeppesen, *unpublished data*; Y. Vadeboncoeur, *unpub-*

lished data). Both models and empirical data indicate that periphyton on sediments can dominate primary production in clear-water shallow lakes at nutrient concentrations up to 100 μg/L of total phosphorus (Vadeboncoeur and Steinmann 2002, Liboriussen and Jeppesen 2003, Vadeboncoeur et al. 2003, 2008). The resilience of the clear-water state dominated by periphyton may be less strong than that dominated by macrophytes, as small changes in turbidity caused by changes in abundance of zooplankton or benthivorous fish may affect capacity of the sediments to retain nutrients. Several more positive feedback mechanisms creating resilience are associated with macrophytes (Moss 1990, Scheffer et al. 1993, Jeppesen et al. 1998). Further field studies and experiments are needed in order to better quantify the effect of periphyton on P release from littoral sediments in a wider range of lakes and the resilience capacity of periphyton.

The role of littoral periphyton in lake food webs is now well established (Hecky and Hesslein 1995, Vadeboncoeur et al. 2001, 2003), and there are more studies that demonstrate the capacity for periphyton to regulate nutrient dynamics in lakes (Spears et al. 2008, Gerhardt et al. 2010). Primary producers are critical regulators of nutrient sequestration and flux in a diversity of ecosystems, including deserts, woodlands, and benthic marine habitats (Scheffer et al. 2001). Most lakes are shallow (Downing et al. 2006) and many are eutrophic because they are situated in low-land areas with high human disturbances. Due to human development and an increasing use of fertilizers, more shallow lakes are expected to reach critical high nutrient levels surpassing the thresholds for alternative states. Furthermore, climate change and increased water demand will alter the water level of shallow lakes throughout the landscape, and changes in water level have shown to be an important factor causing regime shifts (Blindow et al. 1993, Beklioglu et al. 2007). These diverse human effects on the structural and functional relationship between benthic and planktonic habitats require a better understanding of the dynamic role of periphyton in whole-lake ecosystem nutrient cycling in shallow lakes.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for helpful comments on the manuscript. This research was supported by the Japan Society for the Promotion of Science to M. Genkai-Kato. E. Jeppesen was supported by EU REFRESH, CLEAR, and CRES. Y. Vadeboncoeur was supported by the National Science Foundation (DEB 0448682).

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