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## VARIABILITY OF LAKES ON THE LANDSCAPE: ROLES OF PHOSPHORUS, FOOD WEBS, AND DISSOLVED ORGANIC CARBON

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**Abstract.** In northern temperate lakes, algal abundance or chlorophyll levels are affected by phosphorus loading (P), dissolved organic carbon (DOC), and food web effects from trophic cascades induced by anglers. To investigate how changes in land use and climate might affect future chlorophyll conditions in these lakes, we created a nonlinear model for lake chlorophyll that considers the effects of these factors. Parameters were estimated for northern Wisconsin lakes. We show that resilience of the clear-water state in a single lake is maximized when P inputs are low, DOC is high, and angler pressure is low. We simulated a population of lakes to understand the current distribution of chlorophyll and resilience across lakes in the landscape. Under current conditions of land and lake use in the area, the model indicates that most lakes in the region are resilient clear-water lakes. Low chlorophyll levels, however, do not guarantee resiliency. Resilience shows a bimodal distribution suggesting that, with stochastic shocks or changing conditions, more lakes could shift to a high chlorophyll state that is costly to remediate. We also simulated a limnological comparative study to determine what conclusions would be drawn from a common research method if lacustrine ecosystem dynamics are indeed faithfully generated by our model. We show that phosphorus input will most often appear to be the most significant driver of lake chlorophyll levels, despite the fact that all mechanisms (including DOC and grazing) drive the dynamics. This finding suggests that long-standing debates in limnology about the primary drivers of algal abundance are explainable by differences in research approaches. This work brings together community and ecosystem ecology and shows how their processes can interact to drive higher-order feedbacks.

**Key words:** *chlorophyll; dissolved organic carbon; fishing, food web; lakes; landscape; Northern Highlands Lake District, Wisconsin; phosphorus; resilience; variability.*

### INTRODUCTION

Satellite imagery of lake districts reveals astonishing diversity among the apparent color of the lakes, including blue oligotrophic waters, green eutrophic ones, and brown dystrophic lakes. Many of the factors that affect these differences among lakes are known. The rate of phosphorus (P) input affects chlorophyll standing stock, and high levels of P input drive eutrophication (Schindler 1977). Once a lake is sufficiently enriched with P, feedback mechanisms exist that recycle P from anoxic sediments and thereby maintain high chlorophyll levels (Mortimer 1941, 1942, Caraco 1993). Dystrophy in lakes is driven by high inputs of tea-colored dissolved organic carbon (DOC) from the watershed (Rasmussen et al. 1989, Gergel et al. 1999). The concentration of refractory DOC can also vary among lakes because of differences in quantities of wetland area and amounts of littoral vegetation (Wetzel 1990). The colored DOC compounds stain the water and may have their most significant impact on primary

production through shading (Jones 1992). In addition, colored DOC affects the vertical thermal structure of lakes. Lakes with high DOC tend to have shallower thermoclines and less volume for phytoplankton production than those with low DOC (Mazumder and Taylor 1994, Fee et al. 1996). Within lakes, DOC can also reduce primary production by binding essential nutrients such as iron and phosphorus (Jackson and Hecky, 1980, Francko 1986). Food web dynamics also affect chlorophyll levels in lakes (Carpenter et al. 2001). Grazing by zooplankton, and corresponding chlorophyll levels, are strongly related to the size structure of the zooplankton community (Pace 1984, Carpenter et al. 1991), which is in turn affected by size-structured interactions among and by fish (Brooks and Dodson 1965, Mills and Schiavone 1982). The cascading effects of size-structured interactions in the food web can be strongly influenced by fishing (Kitchell and Carpenter 1993, Post et al. 2002).

Regulation of chlorophyll levels has been a primary focus of lake eutrophication studies and water quality management efforts worldwide. The mass of P in epilimnetic chlorophyll is a function of landscape inputs of P, as well as within-lake recycled P from the sediments (Soranno et al. 1997, Carpenter et al. 1998a) (see Plate 1). For many lakes, the rates of recycling are accelerated with increasing chlorophyll because

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PLATE 1. An aerial view of the lake-littered landscape of northern Wisconsin. When viewed from above, these lakes vary in color because of differences in dissolved organic carbon (DOC) and phytoplankton biomass. Both variables are affected by land use patterns. Photograph by S. R. Carpenter.

high chlorophyll in the epilimnion promotes anoxic sediments, which in turn leads to resuspension of sequestered P (Nürnberg 1984). As a result, there can be positive feedback maintaining high lake chlorophyll levels. High P in the water column promotes further inputs of P, even if landscape sources of P have been eradicated (Larsen et al. 1981, Sas 1989, NRC 1992, Cooke et al. 1993). At low P input rates, chlorophyll levels are low, anoxia is rare, and there is little recycling of P from sediments. We can therefore characterize clear- and turbid-water states for lakes, and an important consideration is the resilience of a particular state. Maintaining the resilience of the clear-water state is one goal of lake management (Carpenter et al. 1999). Resilience can be defined as the capacity of a system to remain within a stability domain or state (Holling 1973). An unstable state (or separatrix), at which the system cannot rest, defines the boundary between stable states. The size of the region between the desired stable state and the separatrix represents the resilience of the stable state. Stochastic shocks can shift systems into another state, and the lower the resilience, the more likely is such a shift. In this paper, one of our key interests is to determine resilience of the clear-water state in a population of lakes. This will allow us to assess how vulnerable lakes typical of the Northern Highlands Lake District of Wisconsin might be to entering into the undesired turbid-water state.

While much is known about the processes that control chlorophyll and DOC in lakes, the focal scale of most research has been at the level of the individual lake, even when researchers include many lakes in a given project. Whole-lake experiments are usually aimed at understanding mechanisms for a few similar lakes, for example, and even comparative studies that build regression models using data from a large population of lakes are usually aimed at making predictions for a single target lake (Cole et al. 1991). Yet, populations of lakes exhibit landscape-wide patterns of chlorophyll and DOC (Kratz et al. 1997). Processes

that affect lakes, such as solute inputs and movements of anglers, may have spatially heterogeneous patterns. Understanding spatial patterns of lake chlorophyll or DOC in heterogeneous landscapes will require new approaches (Kratz and Frost 2000). Among these are models capable of summarizing information about landscape patterns for lakes, and making quantitative predictions about such patterns.

We first developed a model of lake chlorophyll incorporating P input, DOC, and food web effects and examined the influences of these variables or drivers on equilibrium chlorophyll values and for resilience of the clear-water state. We then extended the model to populations of lakes influenced by observed distributions of these same drivers. There are several questions we asked with the model: What frequency distribution of chlorophyll should be expected across an ensemble of lakes? What is the frequency distribution of resilience of the clear-water state? How are these distributions controlled by P input, DOC, and fishing? In addition to answering these questions, we had several other objectives in building the model. Crucial mechanisms linking P input, DOC, fishing, and the food web to chlorophyll should be included, yet the model should be simple enough to estimate parameters from routinely available limnological data. We sought a model that could be used as a module or object in landscape-level, individual-based simulations of a lake district.

## METHODS

### *The lake model*

The deterministic lake model predicts areal chlorophyll for a lake, as a function of P inputs, DOC concentrations, and fish harvest. Fig. 1 presents the overall scheme of the model, and parameters are presented in Table 1. It is important to recognize that the metric for our response variable was areal chlorophyll, not volumetric chlorophyll. Managers are interested in controlling visible algal blooms, which are often surface

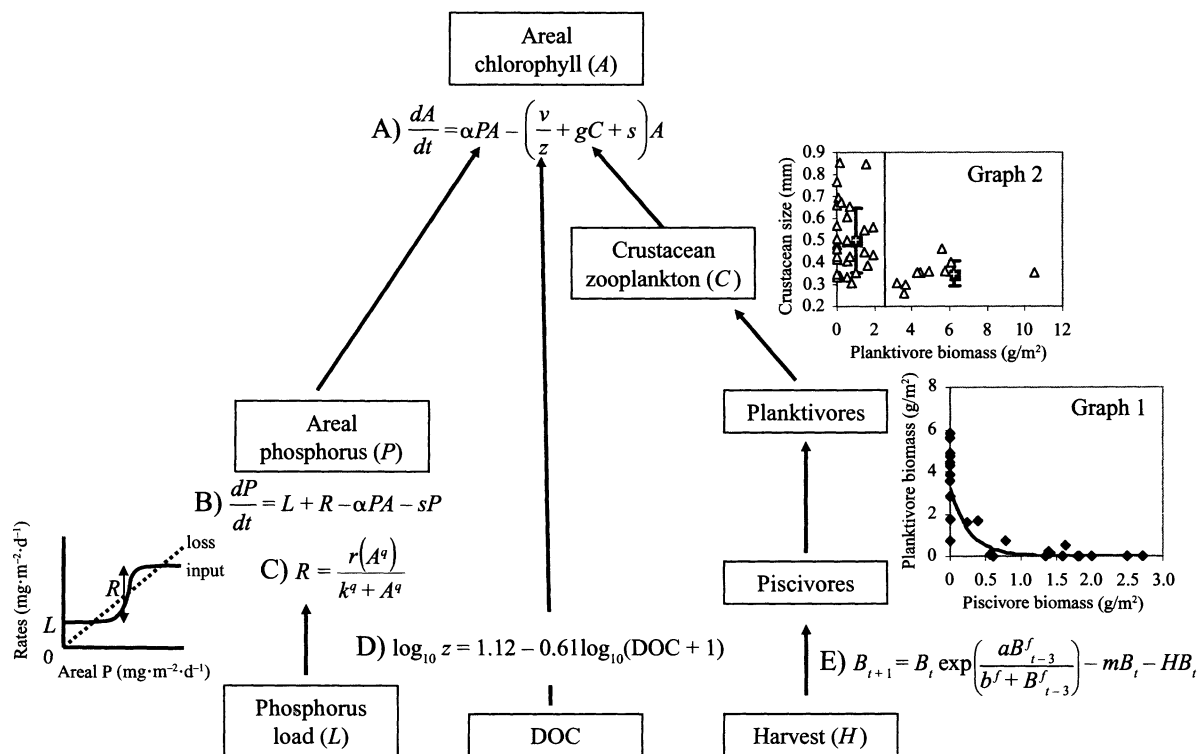


FIG. 1. Overall structure of the lake model showing how the three main drivers of P load (L), DOC, and harvest rates (H) are related to areal chlorophyll (A) through mechanistic and empirical relationships. Variables are defined in Table 1. The source for regression equation (D) is Snucins and Gunn (2000).

TABLE 1. Parameter values, state variables (response variables), drivers, and their associated units as used in the model.

Symbol	Name	Units	Value	Source
<b>Parameters</b>				
<i>f</i>	depensation in piscivores ( <i>B</i> )		2	4
<i>m</i>	natural piscivore mortality	yr <sup>-1</sup>	0.01	1, 3
<i>a</i>	<i>B</i> recruitment shape parameter		0.37	1, 3
<i>r</i>	maximum recycling of P	mg·m <sup>-2</sup> ·d <sup>-1</sup>	8.7	1
<i>q</i>	steepness coefficient for <i>R</i>		8 or 2	1
<i>k</i>	half saturation constant of P recycling	mg/m <sup>2</sup>	90	1
<i>s</i>	flushing rate	d <sup>-1</sup>	0.001	2
<i>b</i>	<i>B</i> recruitment shape parameter		0.5	1, 3
<i>α</i>	maximum growth rate of <i>A</i> per P input rate	mg·m <sup>-2</sup> ·d <sup>-1</sup>	0.8	1
<i>v</i>	sinking rate per algal cell	m/d	0.07	1
<i>g</i>	<i>C</i> grazing coefficient	d <sup>-1</sup>	0.1	1
<b>State variables</b>				
<i>B</i>	piscivore population biomass	g/m <sup>2</sup>		1, 3
<i>W</i>	planktivore population biomass	g/m <sup>2</sup>		1, 3
<i>C</i>	zooplankton community length	mm		1, 3
<i>Z</i>	depth of thermocline	m		5
<i>P</i>	phosphorus	mg/m <sup>2</sup>		output
<i>R</i>	recycled phosphorus	mg/m <sup>2</sup>		output
<i>A</i>	chlorophyll	mg/m <sup>2</sup>		output
<b>Drivers</b>				
<i>H</i>	harvest rate	yr <sup>-1</sup>	0–0.7	input
DOC	dissolved organic carbon	mg/m <sup>2</sup>	adjusted	input
<i>L</i>	P loading	mg·m <sup>-2</sup> ·d <sup>-1</sup>	adjusted	input

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, Carpenter et al. (2001); 2, Cole and Pace (1998); 3, Kitchell and Carpenter (1993); 4, Myers et al. (1995); 5, Snucins and Gunn (2000).

phenomena, and best represented by areal chlorophyll and not a volumetric measure (Carpenter et al. 1999).

The dynamics of algae ( $A$ , milligrams per square meter) (Eq. A in Fig. 1), and phosphorus ( $P$ , milligrams per square meter) in the epilimnion (Eq. B in Fig. 1) were modeled as follows: Areal chlorophyll (amount of algae) depended on growth minus losses. Algal growth was a linear function of  $P$  and standing crop of algae, and losses were from sinking out of the epilimnion, grazing by zooplankton, and flushing. The maximum growth rate of algae per  $P$  input rate was  $\alpha$  (milligrams per square meter per day). Sinking losses ( $v$ , per day) were the sinking rate per algal cell (meters per day) divided by the depth of the thermocline ( $z$ , meters) (Reynolds 1984). The thermocline was determined by lake DOC concentration (Snucins and Gunn 2000; Eq. D in Fig. 1). Grazing losses were determined by the mean body size of the consumer community ( $C$ , millimeters) and a grazing coefficient ( $g$ , per day). Algae and areal  $P$  were exported from the lake via flushing ( $s$ , per day).

The amount of  $P$  in the epilimnion (milligrams per square meter) depends on two inputs:  $P$  loading from the watershed, and  $P$  recycling from the sediment (internal loading). Losses are due to sequestration in algae and flushing. The rate of  $P$  input from the watershed is  $L$  (milligrams per square meter per day). The overall  $P$  recycling rate ( $R$ ) increases in a sigmoid function (Eq. C in Fig. 1) as algal growth increases and causes oxygen to be depleted from the hypolimnion. The maximum rate of  $P$  recycling is  $r$  (milligrams per square meter per day). The exponent  $q$  (dimensionless) affects the steepness of the sigmoid curve at the point of inflection. Larger values of  $q$  give a steeper curve. The value of  $A$  at which recycling reaches half the maximum rate is  $k$  (milligrams per square meter).

Parameters of Eqs. B and C were calibrated to data from experimental lakes (Carpenter and Kitchell 1993, Carpenter et al. 2001) using 36 lake-years of data (Table 1). The fitted model explained 94% of the variance of the observations. Based on a synthesis of the literature, Carpenter et al. (1999) estimated that  $q$  ranges from  $\sim 2$  to 20 for the world's lakes. Our baseline value of  $q = 8$  is similar to the value of 7.9 estimated by Carpenter et al. (1999), using recycling rates reported by Soranno et al. (1997) for Lake Mendota, Wisconsin. Values for flushing rate ( $s$ ) for the experimental lakes were determined by Cole and Pace (1998).

The drivers ( $P$  load, DOC concentration, and angler harvest) affect chlorophyll concentration via direct  $P$  loading and recycling (Eq. B in Fig. 1), DOC effects on thermocline depth (Eq. D in Fig. 1), and propagation through the food web of effects of angling (Eq. E in Fig. 1, and Eqs. 1 and 2). DOC concentrations were used to determine thermocline depth, using a regression for small lakes in Ontario, Canada (year 1999 in Table 4 in Snucins and Gunn 2000). Through the effect of

thermocline depth on  $v$ , DOC affects loss rates of chlorophyll.

The effect of anglers was propagated down the food web to chlorophyll as follows. Piscivorous fish biomass was modeled with depensatory recruitment (Myers et al. 1995) (Eq. E in Fig. 1). Depensation is another term for an Allee effect or inverse density dependence in which recruitment declines as population biomass declines. Removal of piscivorous fish by anglers ( $H$ ) was linear with total piscivore biomass in the lake. Parameters for shaping the depensation function ( $a$ ,  $b$ ,  $f$ ) (Table 1), as well as the natural mortality rate ( $m$ ) of the piscivore population were estimated from fits of the model to largemouth bass populations in Paul Lake, Michigan, from 1991 to 1999 (Carpenter et al. 2001). Our model was solved for equilibrium piscivore biomass for a given level of harvest ( $H$ ). The piscivore population can become extinct from overexploitation when  $H > 0.367$ , or when  $\sim 37\%$  of the population are harvested annually.

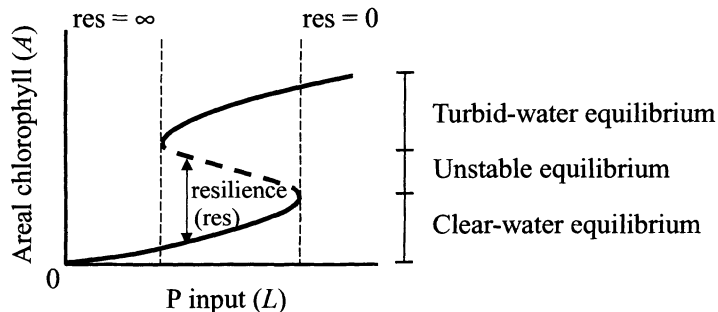
The effects of piscivorous fish on planktivorous fish, and planktivorous fish on zooplankton length, were modeled statistically using data from experimental lakes (Carpenter et al. 2001). There was a negative exponential relationship of piscivore biomass ( $B$ ) to planktivore biomass ( $W$ ):

$$W = 3.2e^{-3.6926B} \quad (1)$$

with  $r^2 = 0.57$  (Graph 1 in Fig. 1). The relationship between zooplankton community length and planktivore fish biomass was also based on the experimental lake data (Carpenter et al. 2001). Zooplankton length ( $C$ ) was high and variable for low planktivore biomass ( $W$ ), and lower and less variable for higher planktivore biomass (Graph 2 in Fig. 1). To represent this pattern, we used a model with a breakpoint in planktivore biomass and two means and standard deviations. The Akaike Information Criterion (AIC) values, which provide estimates of model fits, were much lower for this categorical model (AIC =  $-22.1$ ) than for a log-log regression (AIC =  $+17.18$ ), suggesting that the categorical fit was more appropriate. Maximum likelihood fitting of the breakpoint model determined that if  $W < 2.58$  mg/m<sup>2</sup>, then  $C = 0.50$  mm and if  $W > 2.58$  mg/m<sup>2</sup>, then  $C = 0.35$  mm.

Solutions for steady-state epilimnetic areal chlorophyll across a range of  $P$  loads ( $L$ ) yield either a single stable point (high or low chlorophyll equilibria), or a situation with three steady-states: two stable and one unstable (Fig. 2). In the multiple solution case, one steady state has high chlorophyll, and the other low chlorophyll, with the unstable solution in between. Here, resilience of the clear-water state is the size of the area between the lower stable equilibrium and the unstable equilibrium, where these co-occur. Stochastic shocks that push the system across the unstable boundary will result in a system within the basin of attraction of the upper equilibrium value. Where only the upper

FIG. 2. Alternate states in deterministic runs of the model. Dark solid lines represent stable states with the dashed line joining them indicating the unstable state. The bar to the right of the graph indicates chlorophyll conditions associated with each state. Resilience (*res*) of the clear-water state is the difference between the lower stable state and the unstable one. The *P* input rates corresponding to the limits of infinite and zero resilience are indicated with dashed vertical lines.



stable equilibrium exists, resilience of the clear-water state is assumed to be zero, and where only the lower stable equilibrium exists, resilience of the clear-water state is infinite (Fig. 2).

#### *Stochastic simulations for a population of lakes*

To simulate frequency distributions of chlorophyll for populations of lakes, we randomly selected values of the drivers (*L*, *DOC*, and *H*) from observed distributions, and then calculated distributions of equilibrium chlorophyll and resilience of the clear-water state. Note that these stochastic simulations were not spatially explicit and ignored spatial correlations. They did, however, address the variability that might be expected from inter-lake variation in *L*, *DOC*, and *H*.

We fit lognormal distributions to observed data for each of the main drivers in the model (*L*, *DOC*, and *H*). For *H* fitting, a few extra steps were required. Ten percent of the observed harvest rates were zero, so a lognormal distribution was fit to lakes with nonzero *H*. Then the stochastic simulation was carried out in two stages, first drawing zeroes (10%) from a uniform distribution and then drawing nonzero *H* values (90%) from the lognormal distribution for lakes with nonzero harvest. The drivers *L*, *DOC*, and *H* were sampled from the appropriate normal distributions (*Z*) and then back-transformed to the original units (*N*) using the transformation in Hilborn and Mangel (1997:76, equation 3.76):

$$N = \exp\left(Z - \frac{\sigma^2}{2}\right). \quad (2)$$

To examine effects of correlations among *L*, *DOC*, and *H*, multivariate normal variates were drawn using the appropriate mean vector and covariance matrix, then exponentiated as above. Given a value of *H*, zooplankton size was sampled from the appropriate truncated Student *t* distribution (Ripley 1987). Zooplankton size was truncated at 0.2 mm because smaller values were not observed. All Monte Carlo results reported here are based on 1000 trials.

#### *Data for distributions of L, DOC, and H*

The *L* distribution came from an extensive global data set (Canfield and Bachmann 1981). From this data

set, we excluded lakes with residence times less than one year and reservoirs, both of which are not representative of northern Wisconsin lakes. The *DOC* distributions were gathered from several data sets for northern Wisconsin lakes. A total of 290 *DOC* samples for different lakes were available, most single samples taken in the summer or fall. Data came from the North Temperate Lakes Long-Term Ecological Research site (LTER; *n* = 7; Chemical Limnology data set [available online]),<sup>3</sup> experimental lakes in northern Michigan (*n* = 20; Carpenter and Kitchell 1993, Carpenter et al. 2001), a survey of lakes in northern Wisconsin (*n* = 159; Eilers et al. 1983), the U.S. EPA Eastern Lakes Survey program (ELS; *n* = 88; Glass and Sorensen 1994), and a 1991 survey in northern Wisconsin (*n* = 16; T. K. Kratz, *personal communication*). The distribution of harvest levels on the piscivorous species, walleye, for 210 northern Wisconsin lakes, was obtained from the Wisconsin Department of Natural Resources (DNR) for randomly selected lakes across the state sampled from 1990–1998 (Beard et al. 1997). Harvest rates represent the annual value for a lake in the year it was sampled.

## RESULTS

### *Behavior of a single lake*

The model predicts areal chlorophyll of a lake at steady state, given *P* input (*L*), *DOC* concentration, and harvest rate (*H*). For a single *DOC* concentration and harvest rate (e.g., Fig. 3A), areal chlorophyll generally has two stable states separated by an unstable state. For low levels of *P* inputs, steady state areal chlorophyll is low. However, for higher levels of *P* inputs, *P* accumulates in sediments, causing a positive feedback between *P* recycling and anoxia that produces much higher steady state chlorophyll levels (Carpenter et al. 1999).

The three states of areal chlorophyll that resulted from the model included a low equilibrium (a clear-water state), an unstable equilibrium, and a high stable equilibrium (a turbid or eutrophic state) (Figs. 2 and 3). The critical *P* input rates for transitions between

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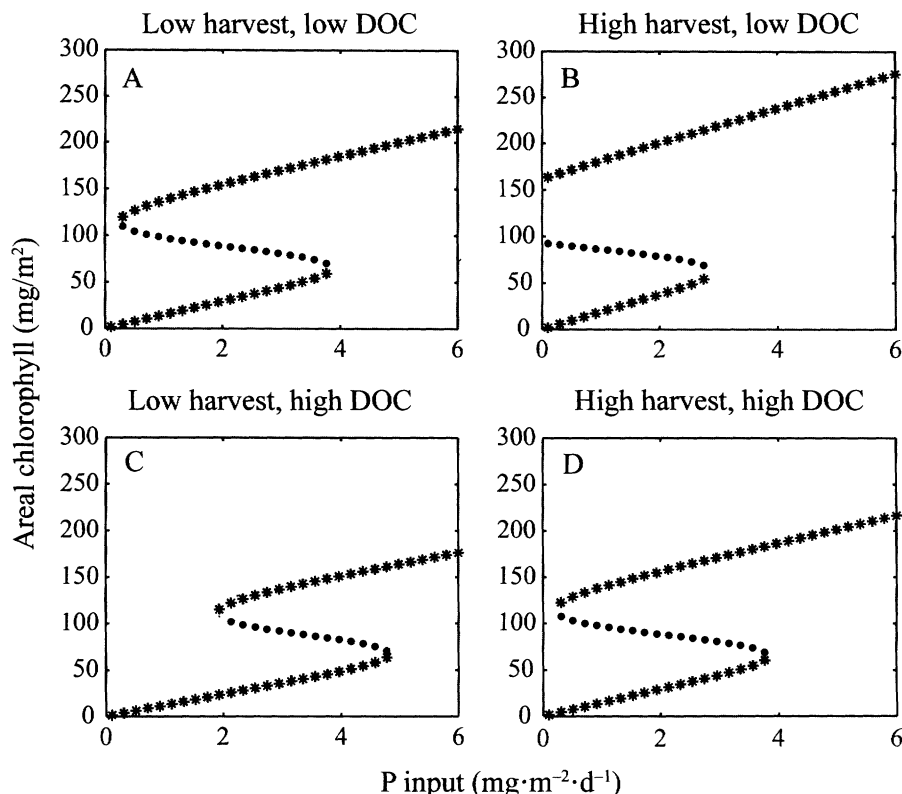


FIG. 3. Areal chlorophyll at steady state vs. P input rate. Both stable (\* symbols) and unstable equilibria (solid circles) are shown. Subplots represent different parameter conditions for (A) piscivore harvest rate  $H < 0.367$  and dissolved organic carbon (DOC) = 6 mg/L, (B)  $H > 0.367$  and DOC = 6 mg/L, (C)  $H < 0.367$  and DOC = 18 mg/L, and (D)  $H > 0.367$  and DOC = 18 mg/L.

low and high chlorophyll depended on DOC concentration and harvest rate. The range of P inputs for which only the clear-water equilibrium exists increases with DOC concentration (Fig. 3C, D). In addition, steady state chlorophyll was somewhat lower for the eutrophic state under higher DOC concentrations. High harvest rates had the opposite effect, reducing the size of the region for which only the clear-water state equilibrium was present. When harvest rates were high (>37% of the population was harvested annually), the piscivorous fish population went extinct and planktivorous fish dominated, leaving a zooplankton community consisting of small inefficient zooplankton grazers that had little impact on chlorophyll levels (e.g., Fig. 3B, D). In contrast, low harvest caused domination of piscivorous over planktivorous fish, leading to a large efficient zooplankton community that had substantial impact on chlorophyll levels (e.g., Fig. 3A, C). For some combinations of low DOC concentration and high harvest, the clear-water state cannot be reached from the eutrophic state for certain levels of P inputs (e.g., Fig. 3B). Such a lake could not revert to a clear-water state even if P input was reduced to zero.

The model can also be described by the resilience of the clear-water state to changes in P input, DOC

concentration, and harvest (defined in Fig. 2). If only the lower equilibrium exists, resilience is infinite for the clear-water state. If only the higher (eutrophic) equilibrium exists, resilience of the clear-water state is zero. If both states exist, resilience of the clear-water state is measured by the difference between the unstable chlorophyll equilibrium and the lower, clear-water equilibrium. The larger the resilience, the higher P inputs, less DOC concentration, and higher harvest can get without causing the lake to switch to a eutrophic state.

Resilience of the clear-water state was highest when harvest was low, DOC concentrations were high, and P inputs were low (<3 mg/m<sup>2</sup>) (Fig. 4). For a given P input or harvest rate, higher DOC concentrations increased resilience, up to infinity for the highest DOC levels. Lower DOC levels increased resilience gradually with each increase in P input. For a given DOC and harvest rate, increasing P input also reduced resilience of the clear-water state. Lower harvest rates promoted higher resilience for respective DOC and P inputs.

The P input rate at which areal chlorophyll switches from the clear-water equilibrium to the eutrophic equilibrium can also be described by the drivers of DOC

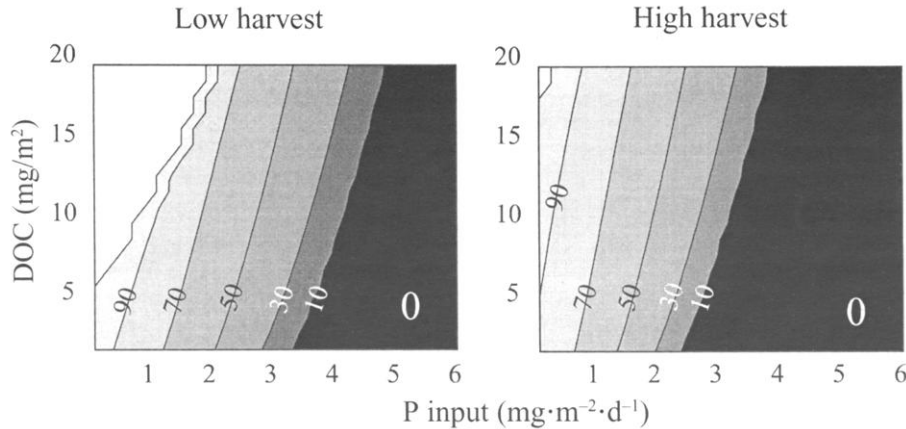


FIG. 4. Contour plots showing resilience of the clear-water state for different P input rates, DOC concentration, and the two levels of piscivore harvest. Lines show equivalent amounts of resilience from 0 to an infinite maximum. Numbers on the lines show values of resilience for that contour. Darker sections indicate lower resilience of the clear-water state.

and harvest (the “flip-up” point; Fig. 5A). The flip-up point increases with DOC concentration (Fig. 5B). Also, the flip-up point is higher when fish harvest is low. Similarly, the P input rate at which areal chlorophyll could be reduced to the clear-water equilibrium (the “flip-down” point; Fig. 5) depended on DOC and

harvest. The flip-down point tends to increase with DOC concentration, and is higher when fish harvest rates are lower. Note also that the flip-up points are generally higher than the flip-down points. That is, the system was hysteretic: much lower P input rates were required to switch the eutrophic, high chlorophyll state to a clear-water state than would be required to maintain the clear-water state.

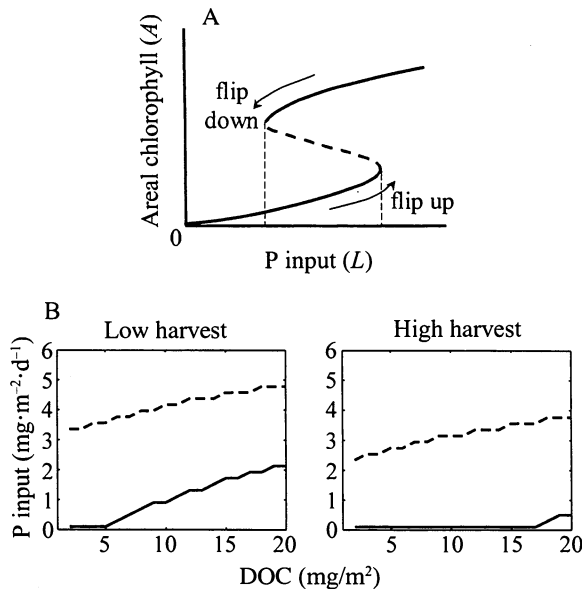


FIG. 5. (A) A stylized case for the relationship between P input rates and areal chlorophyll. Following the lower solid line to the right, as P input increases, a “flip up” in chlorophyll to a turbid state occurs at sufficiently high P levels. Following the upper solid line to the left as P input rates are reduced, a “flip down” to a clear-water state occurs when P input is sufficiently reduced. Note that these flips do not occur at the same P input rate. (B) These graphs show the value of the P input rate at which the system switches between a clear-water state and a turbid state (dashed line = flip up, solid line = flip down) across a DOC concentration gradient and under conditions of low piscivore harvest ( $H < 0.367$ ) in the left graph and high harvest ( $H > 0.367$ ) in the right.

*Behavior of a population of lakes*

We ran a stochastic version of the model with the drivers chosen 1000 times randomly from data distributions for harvest, DOC, and P inputs for northern temperate lake regions. The means and standard deviations for the empirically observed lognormal distributions are presented in Table 2.

When alternate states are possible, there are several ways to consider the distribution of equilibria. First, consider that lakes in the Northern Highlands Lake District currently exist mainly at low P and chlorophyll levels, but may be subject to a flip up to the turbid state as outlined in Fig. 5 when P levels increase. In this case, the distribution of chlorophyll in a population of lakes would resemble that of the dark bars in Fig.

TABLE 2. Mean and standard deviations for the lognormal distributions fit to data for the three model drivers: annual harvest rate ( $H$ ), phosphorus loading ( $L$ ), and DOC, with the number of lakes ( $N$ ) in each independent empirical data set.

State variable	Mean	SD	$N$
$\text{Ln}(H)$	-2.36	0.743	210
$\text{Ln}(L)$	0.357	1.128	252
$\text{Ln}(\text{DOC})$	1.556	0.628	290

Notes: Data were obtained from a global data set for  $L$  (Canfield and Bachman 1981), from various Wisconsin and U.S. EPA data sets for DOC, and from the Wisconsin Department of Natural Resources for  $H$  (Beard et al. 1997).

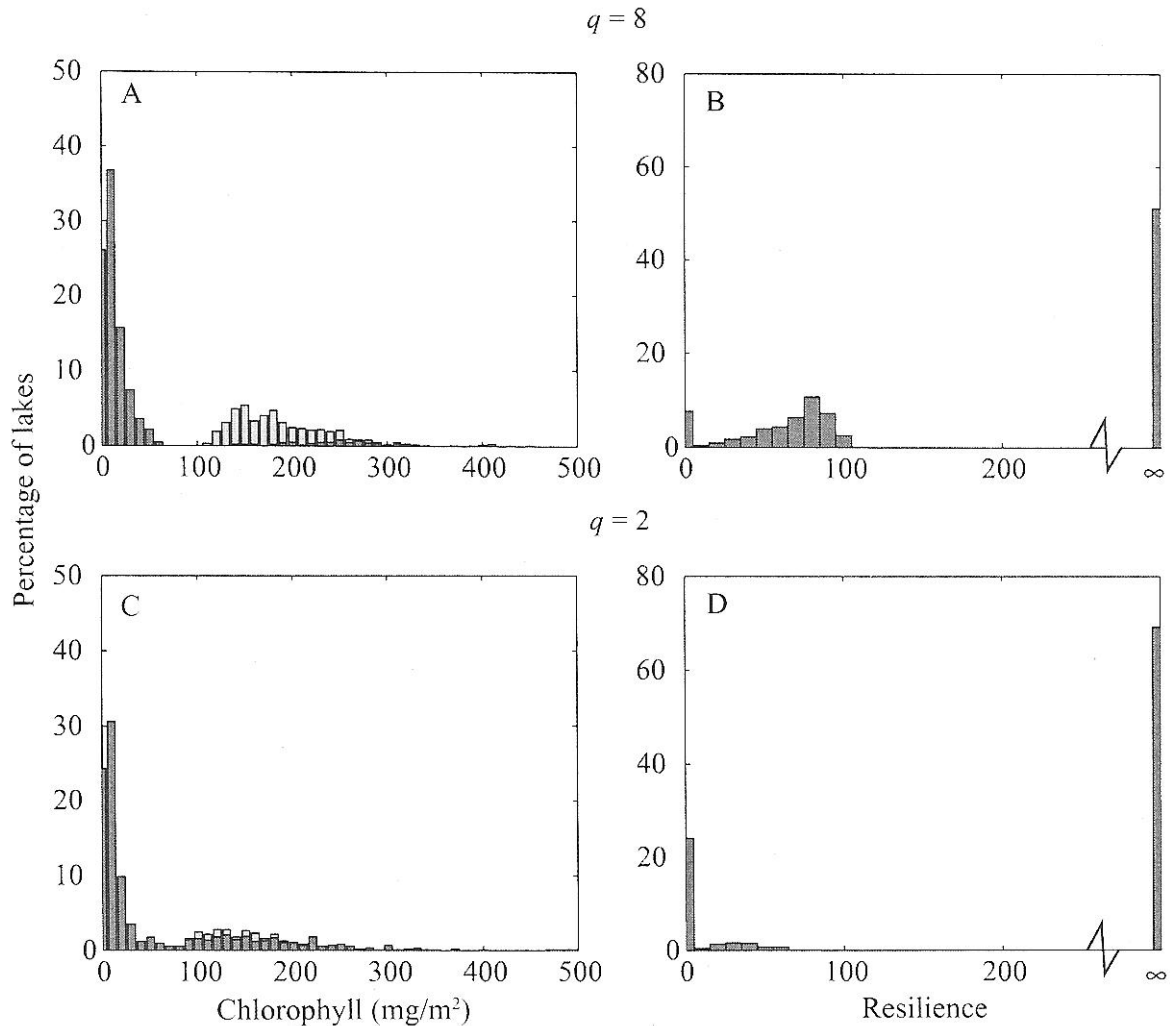


FIG. 6. Distribution of chlorophyll levels for lakes in a low (dark bars) or high (light bars) equilibrium state resulting from the stochastic simulations for 1000 lakes using observed distributions of driver values. The left set of graphs shows the frequency of occurrence of the high and low stable equilibrium points, and the right set of graphs shows the distribution of resilience for these systems (as defined in Fig. 2). Two values of  $q$  (steepness of the P recycling coefficient) were simulated with  $q = 8$  in panels (A) and (B), and  $q = 2$  in panels (C) and (D).

6A. These bars represent choosing the lowest chlorophyll state possible when multiple states exist. However, we can also consider that lakes may have already flipped up to the turbid state, and simultaneously plot the distribution of lakes already in the high equilibrium state. For this we include equilibria values corresponding to the turbid state only when more than one equilibrium is possible. These are the light colored bars in Fig. 6A. On the other hand, we can consider both upper and lower equilibria simultaneously by looking at all bars in Fig. 6A. Examining the existence of all possible states in this case, we see that the frequency distribution of areal chlorophyll was distinctly bimodal, in simulations that used the nominal parameter values (i.e.,  $q = 8$ ). Most lakes were in the clear-water state, consistent with observations of lakes in the Northern Highland region. In most cases, the clear-water state was

highly resilient (Fig. 6B). Zero resilience (permanent eutrophication) was rare in these simulations. Even the eutrophic lakes could potentially be converted to clear water.

Lake morphometry is known to affect anoxia, phosphorus recycling, and chlorophyll (Charlton 1980, Cornett and Rigler 1980, Nürnberg 1998). In our model, the parameter  $q$  (the steepness coefficient for recycled P) is inversely related to lake mean depth (Carpenter et al. 1999). Carpenter et al. (1999) estimate that the plausible range of  $q$  for a wide variety of lakes is  $\sim 2$ – $20$ . To assess the sensitivity of our results to morphometry, we ran a set of stochastic simulations with  $q = 2$ , corresponding to lakes that are generally deeper and more strongly stratified than under our nominal parameters. A lower  $q$  corresponds to an unfolding of the S-curve depicted in Fig. 2.

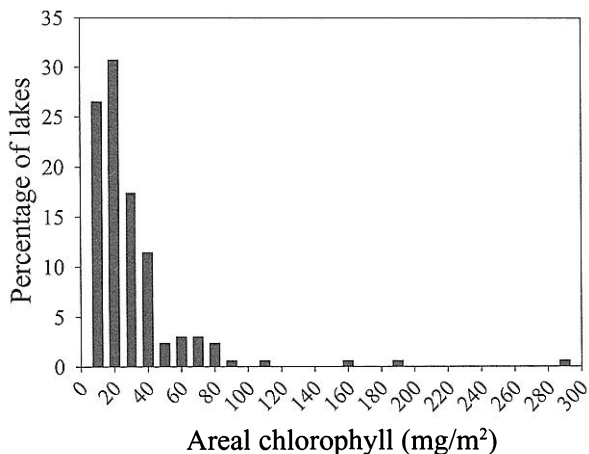


FIG. 7. Observed areal chlorophyll distribution for 166 lakes in northern Wisconsin. Data represent single samples taken during the open water season and are a subset of the lakes for which DOC data distributions were obtained as outlined in the *Methods*. These data were collected through the North Temperate Lakes LTER, experimental lakes (Carpenter et al. 2001), a survey of Wisconsin lakes (Eilers et al. 1983), and the U.S. EPA Eastern Lakes Survey (Glass and Sorensen 1994).

With  $q = 2$ , the distribution of areal chlorophyll concentrations no longer displays two modes (Fig. 6C). Rather, it resembles the unimodal distribution we actually observe in the Northern Highland Lake District (Fig. 7). However, the distribution of resilience for the clear-water state remains strongly bimodal (Fig. 6D). Many clear-water lakes have infinite resilience, i.e., effects of P inputs are quickly dampened and the clear-water state is maintained. Other lakes, which appear to be drawn from the same unimodal chlorophyll distribution, have clear-water states that are much less resilient, with many more now having zero resilience. This result shows that an apparently homogeneous distribution of chlorophyll on a landscape may belie large differences in resilience.

On real landscapes, the drivers (input rate of P, DOC, and harvest of game fish) will be correlated. How might these correlations affect our results? We do not have data to measure the correlations among drivers, but we know the likely sign of the correlations. P and DOC inputs derive from some of the same hydrologic and landscape factors, and are likely to be positively correlated. Anglers tend to avoid stained lakes, but may prefer slightly enriched lakes (T. D. Beard, *personal communication*). To examine the potential effect of such correlations, we performed simulations with  $r = -0.5$  between DOC and harvest,  $r = 0.3$  between  $L$  and harvest, and  $r = 0.5$  between  $L$  and DOC. The correlations have little impact on the frequency distributions of chlorophyll and resilience and they are not shown because the resemblance to Fig. 6 is so striking.

How would a population of lakes generated by our model be interpreted by comparative limnologists? To

examine this issue, we simulated another 150 000 lakes with correlated drivers from which our “simulated limnologists” could choose to sample. We had 500 “limnologists” each sample 30 lakes at random (with replacement), so that a total of 15 000 of the lakes were sampled for chlorophyll ( $A$ ), phosphorus input ( $L$ ), DOC, and zooplankton community length ( $C$ ), which is an index of harvest rate by anglers or  $H$ . We chose  $n = 30$  because that is a typical sample size for a comparative study, and large enough that the Student  $t$  distribution of errors (26 df) is close to the normal distribution. Each “limnologist” then performed a multiple regression of the form

$$\ln(A) = \beta_0 + \beta_1 \ln(L) + \beta_2 \ln(C) + \beta_3 (\text{DOC}) \quad (3)$$

that represented the best fitting model to the entire data set and where  $\beta_i$  represent the coefficients to be fit. The  $t$  statistic for each regression parameter was recorded. We plotted the frequency distributions of the  $t$  statistics for each parameter estimated in the model. The frequency distributions of drivers’ ( $L$ ,  $C$ , and DOC)  $t$  statistics (Fig. 8) show that phosphorus loading ( $L$ ) is the driver that would be most often appear to be driving the landscape pattern of chlorophyll levels. The effect is especially strong in the  $q = 8$  scenario (where 100% of the regressions were significant), but  $L$  also appears as the most important driver in the  $q = 2$  scenario where 88.6% of regressions were significant. Zooplankton length ( $C$ ) is also a significant driver in many of the regressions (28.2% with  $q = 8$ , 12% with  $q = 2$ ). DOC appears only rarely (1.4%) as a significant driver when  $q = 8$ . The same general pattern, i.e., a dominant phosphorus signal, with some evidence for grazing impacts, was observed for the uncorrelated driver simulations. If a large sample of lakes is drawn, all driver effects are significant, but comparative limnological studies are often done with <100 lakes.

## DISCUSSION

### *Model evaluation*

Our lake model is a useful representation of several empirically known properties of lakes. For example, in model runs, chlorophyll responds to P input, DOC, and fish harvest in ways that are consistent with empirical evidence. The model allows the calculation of areal chlorophyll using three important drivers (P input, fish harvest, and DOC) in a simple, repeatable, and transparent way. The parameters can be estimated from available data for the Northern Highlands Lake District of Wisconsin. The model represents the hysteresis of eutrophication known from many studies (Cooke et al. 1993, Nürnberg 1998, Carpenter et al. 1999), in which the response of the system to an increase in resource input is different from the response of the system to a decrease in the same resource. Therefore, it is possible to calculate resilience of the clear-water state, an important characteristic for predicting future changes in

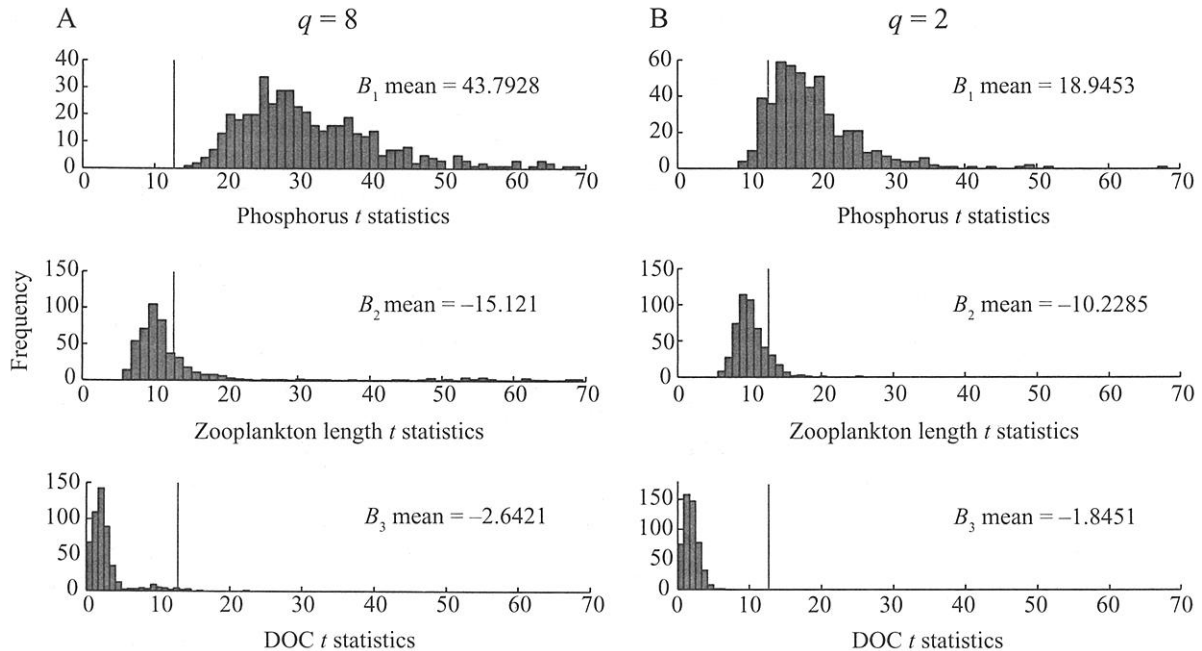


FIG. 8. Frequency distributions of the absolute values of the *t* statistics for each component (*L*, *C*, and DOC) of the multiple regressions of 30 lakes taken 500 times from a total simulated lake landscape of 150 000 lakes from the model in Fig. 1 for  $q = 8$  and  $q = 2$ . Bars to the right of the vertical line in each plot represent significant values at  $P = 0.05$  ( $df = 1$  for each parameter estimate). Mean values for each estimated coefficient ( $\beta_i$  in Eq. 3) represented by the *t* distributions from all 500 regressions are also indicated on the plots.

the lake (Scheffer 1997, Carpenter et al. 1999). The model is designed to be used as a module within a larger landscape model of lakes. Consequently, it is possible to use stochastic simulations to examine the properties of a population of lakes on a landscape. With appropriate parameter choices (e.g.,  $q = 2$ ), the frequency distribution of chlorophyll obtained from the model resembles observations from the Northern Highlands Lake District. These simulations show that even an apparently unimodal distribution of chlorophyll levels may hide bimodalities in resilience. Lakes with low resilience are vulnerable to eutrophication by increased P input, and the frequency of vulnerable lakes on a landscape may be hidden in surveys that measure only the chlorophyll distribution.

On the other hand, the model has important limitations that must be acknowledged. Most of our parameter estimates are based on the Cascades experimental lakes (Carpenter and Kitchell 1993, Carpenter et al. 2001) in the Northern Highlands Lake District of Wisconsin and Michigan, and may not be appropriate for other lake districts. In particular, the relationship between piscivore and planktivore biomass is derived from whole-lake experiments on bass–minnow communities (Carpenter et al. 2001). Its applicability to a wider range of fish community structures is unknown. Other planktivores (e.g., gizzard shad) can show a size refuge as they grow or use alternative prey efficiently (Stein et al. 1995, Dettmers and Stein 1996). To extend these results, data would be needed for relationships

of planktivore to piscivore biomasses for a wider variety of fish communities.

We have also simplified certain relationships. A linear conversion factor of P to algal biomass is assumed, and no algal species-related effects such as the development of inedible algae populations are modeled. These should be considered for future studies. Similarly, the potential effects of variations in nitrogen loading are not considered. The response of zooplankton body size to planktivore biomass was expressed as a categorical response rather than as a smooth curve. Categorical responses allowed us to account for different variances with mean zooplankton lengths in the stochastic runs. As a consequence of this categorical model, harvest rates resemble a toggle switch for the choice of mean zooplankton length and the resultant grazing rate ( $g$ ). When harvest rates were above a critical value ( $H > 0.367$ ), piscivore populations were reduced and planktivore populations were high, resulting in the choice of the smaller zooplankton length mean. The opposite relationships hold for low harvest rates. A better understanding of why and how variances differ for zooplankton communities of different mean sizes is worthy of further exploration.

By expressing results as vertically integrated chlorophyll, the model avoids the complications of the vertical distribution of chlorophyll. However, this vertical distribution may be important, both for lake primary productivity and for management (St. Amand and Carpenter 1993, Christensen et al. 1995). For example,

metalimnetic production may be important in lake nutrient budgets, but not apparent to lake users concerned with water clarity. Also, the vertical structure of phytoplankton may depend on a complex of factors that affect stratification, mixing and light transmission (Kalf 2001, Diehl 2002). While a number of models exist for vertically structured phytoplankton dynamics, we consider this phenomenon to be outside the scope of this study.

The model does not explicitly account for hydrologic drivers, such as flushing rate, or morphometric factors such as mean depth. Instead, these important features of lakes are implicit: They affected the parameter values we estimated for the Northern Highlands Lake District, but do not appear explicitly in the equations. We used sensitivity analyses (e.g., Fig. 6 and correlated driver simulations) to assess the potential impact of morphometry and correlated hydrologic inputs on the patterns discussed in this paper. However, extension of the model to landscape calculations will probably require a more explicit treatment of hydrology and morphometry. Lake morphometry can influence rates of recycling, and a number of formulations for such models have been published (Carpenter 1983, Chapra and Reckhow 1983, Nürnberg 1998). The strength of trophic cascades can also be affected by morphometry, with deeper lakes characterized by zooplankton communities with larger body size and less edible phytoplankton than shallower lakes, where little refuge from fish zooplanktivory exists (Tessier and Woodruff 2002).

#### *Limnological lessons*

The results of our stochastic simulations of the baseline lake model predict a bimodal distribution of lake chlorophyll levels across a landscape with a gap between the high and low chlorophyll stable states (Fig. 6,  $q = 8$ ). This gap represents the non-feasible unstable equilibrium. If we consider most lakes on the landscape in the Northern Highlands Lake District of Wisconsin to currently be in the clear-water state with potential exposure to higher landscape P levels with land use change, the distribution resembles the empirical one (i.e., only considering the dark bars in Fig. 6A). However, many of these lakes have low resilience of the clear-water state (Fig. 6B).

Empirically, we see a similar lognormal distribution but no obvious gap in observed chlorophyll levels (Fig. 7). There are several possible reasons for this discrepancy between model output and observed data. One possibility is parameter uncertainty. If we set  $q = 2$ , we obtain a unimodal distribution similar to the observations (Fig. 6C). The data do not exist for a more refined estimate of  $q$ . Another possible explanation for the discrepancy lie in the data and in the rate of approach to steady state. The chlorophyll data shown in Fig. 7 are not necessarily summer averages or steady-state values, but represent arbitrarily chosen single

samples during the ice-free season. Noise in the data could hide bimodality that may be revealed by a more intensive sampling program.

Unlike the bimodality of chlorophyll levels, the prediction of bimodal resilience distributions is robust to parameter choice. Our analysis suggests that some of the lakes in the Northern Highlands Lake District are vulnerable to eutrophication, because the resilience of the clear-water state is low. Furthermore, our analysis suggests that chlorophyll may not be a good indicator of resilience. Assessing resilience requires a deeper analysis that considers, for example, potential for P recycling, DOC, and food web structure.

Models focusing exclusively on shallow non-stratifying lakes also predict alternative states for lake chlorophyll levels (Scheffer et al. 1993, Jeppesen et al. 1999). Our work here and elsewhere (Carpenter et al. 1999) shows that catastrophic shifts between clear and turbid lake states may also occur in deeper, stratified lakes. The effect of the nutrient recycling rate parameter  $q$ , which is mainly a function of lake morphometry, herein shows that the likelihood of a bimodal distribution of lake states is greater in shallower lakes. However, the resilience of chlorophyll states is always bimodal. Our model extends previous work on shallow lakes by showing that stratifying lakes may have hysteretic chlorophyll states and by determining the distributions of chlorophyll levels across a landscape of many lakes.

Among the most important results of this modeling exercise is the fact that the drivers one would conclude as explanatory for a single lake (the deterministic model) would differ from those for a distribution of lakes across a landscape (the stochastic models). Diverse lines of evidence show that fish harvest rates, DOC, and P inputs are all important drivers of lake chlorophyll levels (Carpenter and Kitchell 1993, Carpenter et al. 1998b, 2001). At the landscape level, comparative studies analogous to our stochastic model runs would conclude differently. In comparative studies of 30 lakes, P input appears as the most important driver of observed chlorophyll levels, despite the fact that food web and DOC effects are explicitly included in the model. That P input is the major driver of lake chlorophyll has been a common conclusion of comparative studies of lakes (Rigler and Peters 1995). Our model shows how multiple mechanisms acting at the scale of single lakes lead to statistically dominant effects of phosphorus at landscape scales.

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