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Dystrophy and Eutrophy in Lake Ecosystems: Implications of Fluctuating Inputs

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## MINI- REVIEW

**Minireviews** provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

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# Dystrophy and eutrophy in lake ecosystems: implications of fluctuating inputs

Stephen R. Carpenter and Michael L. Pace

Carpenter, S. R. and Pace, M. L. 1997. Dystrophy and eutrophy in lake ecosystems: implications of fluctuating inputs. – *Oikos* 78: 3–14.

Eutrophic and dystrophic states of lake ecosystems are associated with distinct differences in phosphorus (P) input, refractory dissolved organic carbon (RDOC) input, and certain internal processes. Eutrophic lakes have high P input and high primary production. Dystrophic lakes have high RDOC input. In both types of lake, bacterial metabolism may help reduce RDOC levels. In dystrophic lakes, bacterial metabolism may be suppressed by low pH, and primary production is reduced due to light attenuation by RDOC. We analyzed several simple models to ask whether eutrophy and dystrophy are alternative stable states of lake ecosystems. In-lake processes could create alternative states under certain circumstances, but more likely watershed processes maintain eutrophy or dystrophy through contrasts in inputs of P and RDOC. Simulations suggest that pulses of RDOC result in dystrophic conditions that reverse very slowly. Land-use changes or climate fluctuations that change RDOC input rates may have long-lasting effects on trophic state of temperate and boreal lakes. Lack of information on microbial degradation of RDOC, and the dependency of degradation rate on RDOC levels, primary production, and pH, are major sources of uncertainty in our analysis and are suggested as priorities for further research.

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Recent interest in human-induced climate change has prompted research into potential responses of ecological systems (Gates 1993, Kareiva et al. 1993). However, the ecological importance of global climate change is less certain than many other human impacts on the biosphere (Vitousek 1994). We do not know the magnitude, timing or exact direction of climate change (Schneider 1993, McKnight et al. 1996). We can assume that climate will continue to vary, but we do not know if the

human-altered climate of a given region will approach a stable probability distribution or continue to shift for an extended period of time. Thus ecologists must consider the dynamic responses of ecosystems to diverse climate trends as well as to shorter-term climate fluctuations.

Ecologists must also define the key features of ecosystems that enable us to understand, measure, and explore their dynamic variation. One way that limnologists have approached this goal is to identify the key drivers and

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indicators of lake trophic state. Processes that maintain the classically recognized states of oligotrophy (low productivity, low humic content and clear water), eutrophy (high primary productivity, low humic content and green water), and dystrophy (low productivity, high humic content and brown water) are the subject of a rich and complex literature (Wetzel 1983). Certain feedbacks within lake ecosystems tend to maintain trophic states (Wetzel 1983). For example, hypolimnetic anoxia promotes phosphorus recycling from sediments to the epilimnion in certain lakes, thereby helping maintain eutrophy (Mortimer 1941, 1942, Caraco 1993). In other lakes, high levels of refractory dissolved organic carbon suppress bacterial activity and help to maintain dystrophy. These and many other feedbacks support the view that trophic states are alternative stable states of lakes (Holling 1973, Scheffer 1991). However, over time both in-lake processes and inputs to lakes from surrounding ecosystems can change the trophic states of lakes (Lindeman 1942, Wetzel 1983). Material flows from land critically affect trophic state (Hasler 1975, Hynes 1975, Likens 1984, Wetzel 1990). Inputs of phosphorus (P), a limiting nutrient, are a well-understood driver of lake eutrophication (Schindler 1977). Inputs of dissolved organic carbon (DOC), especially refractory DOC (RDOC) or humic compounds, are the main driver of dystrophy (Wetzel 1990).

Like all ecosystem phenomena, trophic state results from the interaction of external forcing and internal processes. But what level of forcing is necessary to change ecosystem state? Conversely, to what extent can internal processes buffer ecosystem state against fluctuations in external forcing? These fundamental questions of ecosystem ecology are also important in the management and restoration of lakes (National Research Council 1992). Changes in climate could affect both inputs and lakes' internal dynamics (Firth and Fisher 1991, McKnight et al. 1996). Climate has powerful effects on lake ecosystems through fluctuations of precipitation and evapotranspiration, which alter inputs of water and solutes (Schindler et al. 1990, Carpenter et al. 1992a, b, Webster et al. 1996). Changes in water flux through lakes alter the cycling of P and degradation of DOC in lakes (Schindler et al. 1990). Land-use changes which alter P and DOC inputs to lakes are already having powerful effects. The resulting variation in P and RDOC concentrations could alter lake trophic state.

This paper asks whether eutrophy and dystrophy are alternative stable states, maintained by internal processes within a particular range of P and RDOC inputs. The contrasting hypothesis is that eutrophy and dystrophy are merely poles of a continuum, maintained by the relative magnitude of P and RDOC inputs but little affected by internal processes. We address this question using the literature, models, and data from a whole-lake experiment.

## Evidence of P-DOC interactions from the literature

While a great deal of research has focused on effects on lakes of P input, limnologists have also recognized the importance of DOC inputs (Birge and Juday 1927, Wetzel 1983). Dystrophic lakes are a significant constituent of temperate and boreal landscapes (Eilers et al. 1988, Wilander 1988, Kortelainen 1993). In southern Finland, for example, about 60% of the lakes have  $\text{DOC} > 10 \text{ mg L}^{-1}$  (Kortelainen 1993). Despite the importance of dystrophic lakes, our knowledge of the causes and consequences of DOC gradients for lake ecosystems is limited in comparison to current understanding of nutrient input gradients (Wetzel 1992).

Organic carbon input rates can be largely independent of nutrient input rates to lakes (Meili 1992). However, the P and DOC pools of the lake interact (Fig. 1). P inputs support growth of phytoplankton, which may be grazed, lost to sediments, or flushed from the lake. A fraction of phytoplankton production is added to the water column as labile DOC (Baines and Pace 1991). Labile DOC is a heterogeneous mix of compounds that are readily metabolized by bacteria suspended in lake water (Søndergaard and Middleboe 1995). DOC also enters the lake from the watershed, surrounding wetlands, and littoral vegetation (Wetzel 1990). An important fraction of this DOC, refractory or recalcitrant DOC (RDOC), is broken down relatively slowly by microbes and through photolytic effects of light (Wetzel et al. 1995). RDOC includes high molecular weight organic acids which lower pH and can inhibit microbial activity (Wetzel 1983, Jones 1992, Schindler et al. 1992, McKnight et al. 1994).

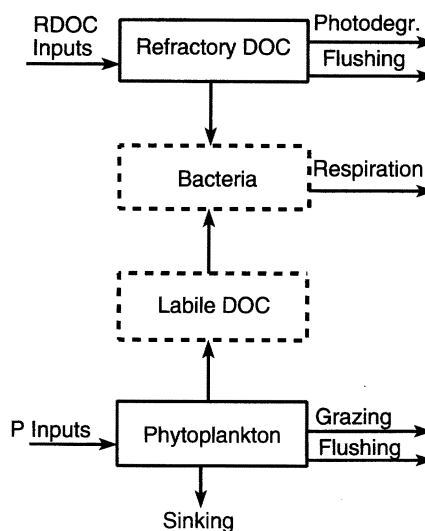


Fig. 1. Flow chart of the modeled interactions of phytoplankton and refractory dissolved organic carbon in lakes.

RDOC also stains lake water and thereby shades phytoplankton, reducing primary production (Jones 1992). By binding inorganic nutrients, RDOC may affect their availability to plankton (Jackson and Hecky 1980, Francko 1986). RDOC is lost from the lake by photodegradation, flushing, and microbial breakdown.

There is increasing evidence that at least some portion of RDOC is degraded biologically in lake water. Many lake carbon budgets reveal that more DOC enters lakes than leaves on an annual basis (Wetzel and Otsuki 1974, Schindler et al. 1992). Much of the annual DOC input appears to be degraded or sedimented (via mechanisms such as flocculation and coagulation), indicating that within-lake processes significantly influence DOC dynamics. Respiration exceeds primary production in the pelagic zones of many lakes (del Giorgio and Peters 1993, 1994). Degradation of RDOC inputs probably accounts for some of this imbalance. Experimental studies of bacterial cultures also provide evidence that RDOC is degraded within lakes and potentially represents a significant energy source. Degradation of RDOC may occur by cometabolism, which is defined as metabolism by a microorganism of a compound that the cell is unable to use as a source of energy or as an essential nutrient (Alexander 1994). De Haan (1977) was among the first to demonstrate the potential of cometabolism in lake systems, through experiments in which addition of benzoate allowed the degradation of fulvic acids by bacteria. Degradation of RDOC is typically enhanced in bacterial cultures derived from natural waters when either nutrients or labile carbon substrates (e.g. glucose) are added (De Haan 1993, Zweifel et al. 1995). RDOC may also serve directly as an energy source. For example, bacteria will grow in cultures where only humic acids are provided as carbon sources (Moran and Hodson 1990) and will also grow on the high molecular weight fraction of DOC (Tranvik 1992, Amon and Benner 1994). These results indicate that bacteria not only metabolize humics and other complex components of RDOC, but are also capable of synthesizing some of this material into new biomass.

The lake trophic states of interest for this paper (oligotrophy, eutrophy and dystrophy) can be characterized by two of the state variables in Fig. 1, phytoplankton biomass and RDOC. These state variables have much longer turnover times than labile DOC and bacteria (Hobbie 1992). We consider lake trophic states at the time scale of a growing season in temperate lakes. For this goal, the appropriate indicators are the two slower variables, phytoplankton biomass (measured as chlorophyll) and RDOC (measured as total DOC). We now turn to the data and models used to investigate the possibility of alternative states in the chlorophyll-RDOC interaction.

## Limnological data

We will use results from a whole-lake experiment, which provides data for fitting models and serves as an example of variability in lake state as a consequence of altered DOC inputs. Long Lake (89° 32' W, 46° 13' N) was divided by two plastic curtains in May 1991, separating East and West basins by a central basin (Carpenter et al. 1996). Dividing the lake separated sources of DOC, causing the DOC concentration of East Long Lake to increase from about 7.5 mg L<sup>-1</sup> in 1991 to more than 14 mg L<sup>-1</sup> in 1993 while the DOC concentration of West Long Lake decreased slightly (Christensen et al. 1996). After 2 years of study (1991 and 1992), both East and West Long lakes were enriched with inorganic nitrogen and phosphorus (N:P 25 by atoms) during summer stratification in 1993 and 1994 (Carpenter et al. 1996). Thus our data for Long Lake from 1991–1994 span a wide range of DOC levels and P input rates.

East and West Long lakes were sampled weekly during the summer stratified seasons of 1991–1994 (Carpenter et al. 1996). Model analyses presented below require data on P input rate, chlorophyll *a*, DOC, respiration and zooplankton size. P input rate was estimated from changes in standing stock, sedimentation, and outflow in 1991–1992 and measured directly in 1993–1994 (Carpenter et al. 1995, 1996). Chlorophyll *a* in the photic zone (above 5% of surface irradiance) was measured at 5 depths and integrated vertically (Carpenter et al. 1996). DOC concentration was measured in the epilimnion (Christensen et al. 1996). Respiration was measured by O<sub>2</sub> consumption in dark bottles (Pace 1993). The method measures total plankton respiration of both autotrophs and heterotrophs. We assume that bacterial degradation of DOC is proportional to total respiration. Mean length of crustacean grazers was measured as an index of potential grazing loss (Carpenter et al. 1996).

## Models

We used two complementary modeling approaches to investigate the possibility of alternative states. Simple statistical models were used to test directly for alternative states. Recently, ecologists have found that complex dynamics can be resolved by fitting relatively simple models to time series (Ellner and Turchin 1995, Ives 1995). Our analyses are prompted by these examples. The statistical-model approach depends only on observed time series, and cannot take advantage of other information about the relevant ecological interactions. We also developed a more mechanistic model, in order to incorporate literature information and more of our own data. The mechanistic model involves more assumptions than the regression analyses, but also in-

cludes more information. The mechanistic model can also be used for simulation studies of ecologically interesting scenarios.

### General models to test for alternative states

We used three simple statistical models to test for the existence of alternative stable states in observed time series: a Bayesian estimate of the probability of alternative states; comparison of polynomials; and comparison of autoregressions. All three approaches employ relatively simple, general models that could be fit to a wide variety of ecological time series.

The Bayesian approach estimates the probability of two stable states in time series data. The estimate is computed from the posterior probability distribution of the parameters  $b_i$  of a cubic polynomial fit to an observed time series  $X$ :

$$\log(X_{t+1}/X_t) = b_0 + b_1X_t + b_2X_t^2 + b_3X_t^3 \quad (1)$$

We assumed independent, noninformative prior distributions for the  $b_i$  and the log of the residual standard deviation,  $\sigma$  (Box and Tiao 1973). The joint distribution of the  $b_i$ s is a multivariate  $t$ -distribution centered on the maximum likelihood estimates with covariance matrix  $\sigma^2(\mathbf{X}'\mathbf{X})^{-1}$  and degrees of freedom  $n - 4$  where  $n$  is the number of observations in the time series (Box and Tiao 1973). In the covariance expression,  $\mathbf{X}$  is the design matrix with columns 1,  $X_t$ ,  $X_t^2$ ,  $X_t^3$ .

Eq. 1 can have one real root (a stable point) or three real roots (of which two are stable points), depending on the values of the  $b_i$ . We estimated the probability of three real roots by Monte Carlo sampling of the posterior distribution. 10 000 parameter sets were drawn randomly from the posterior distribution, and the number of real roots was determined for each parameter set. The proportion of parameter sets having three real roots estimates the probability that the time series exhibits alternative stable states.

The second approach compared the contrasting polynomial models

$$\log(X_{t+1}/X_t) = b_1(X_t - b_2)(X_t^2 + b_3X_t + b_4) \quad (2)$$

and

$$\log(X_{t+1}/X_t) = b_1(X_t - b_2)(X_t - b_3)(X_t - b_4) \quad (3)$$

where  $X_t$  is the time series for the state variable and the  $b_i$  are real-valued parameters estimated by fitting the models to the data. Eq. 2 is the more general model. It has one equilibrium or three (of which two are stable), depending on whether the roots of  $X_t^2 + b_3X_t + b_4$  are real or complex. Eq. 3 is a more restrictive model because it must have three real roots. If eq. 2 fits the

data much better than eq. 3, then we have evidence against the existence of alternative stable states. Goodness of fit was compared using a likelihood ratio test (Gilchrist 1984).

The third approach compared the contrasting autoregressive models

$$X_{t+1} - b_1 = b_2(X_t - b_1) \quad \text{if } X_t > b_3 \quad (4a)$$

$$X_{t+1} - b_4 = b_5(X_t - b_4) \quad \text{if } X_t \leq b_3 \quad (4b)$$

and

$$X_{t+1} - b_1 = b_2(X_t - b_1) \quad (5)$$

where, as before,  $X_t$  is the time series for the state variable and the  $b_i$  are real-valued parameters estimated by fitting the models to the data. Eqs 4a and 4b are the more general model. The system fluctuates around one of the two means,  $b_1$  or  $b_4$ , depending on the position of  $X_t$  relative to the threshold  $b_3$  (Tong 1990). Eq. 5 restricts the system to fluctuation around one mean,  $b_1$ . If eqs 4 fit much better than eq. 5, then we have evidence for dual states. Goodness of fit was compared using a likelihood ratio test (Gilchrist 1984) and an extra sum of squares test (Bates and Watts 1988). The latter test evaluates the null hypothesis that the additional parameters present in eq. 4 but not eq. 5 are zero.

### Mechanistic model of chlorophyll-DOC interactions

We developed a mechanistic model of chlorophyll-DOC interactions that exhibits alternative stable states for certain combinations of parameter values. We then estimated parameters from the literature and from our own data to examine the possibility of alternative stable states.

We attempted to develop a relatively simple model that could exhibit alternative stable states and was consistent with major mechanisms reported in the literature. A further requirement was that it be possible to estimate parameter values from the literature and our data. More complex models with more mechanistic detail could easily be devised. However, it seems appropriate to first investigate alternative states with simple models which are easily understood and fit to data, and later invoke more complicated models if they are necessary.

The model consists of two coupled differential equations, one for areal chlorophyll and one for RDOC concentration:

$$dA/dt = rA[1 - (A/u)][s/(s + R)] - lA \quad (6)$$

$$dR/dt = I - pR - [cARh^2/(h^2 + R^2)] \quad (7)$$

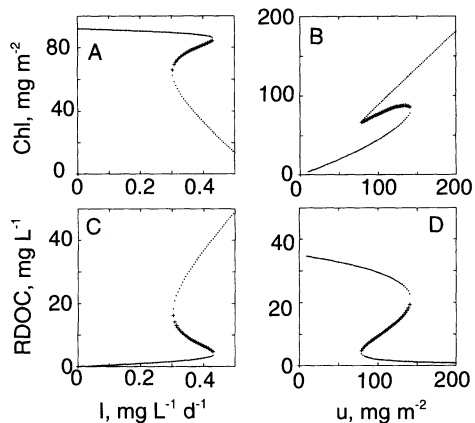


Fig. 2. Equilibrium points for areal chlorophyll (A, B) and refractory dissolved organic carbon (C, D) across gradients of RDOC input rate  $I$  (A, C) and maximum areal chlorophyll  $u$  (B, D). Dots are stable equilibria; crosses are unstable equilibria. Parameter values:  $r = 1$ ;  $u = 100$ ;  $s = 5$ ;  $l = 0.08$ ;  $I = 0.35$ ;  $c = 0.002$ ;  $h = 4$ ;  $p = 0.01$ .

The state variables are  $A$  (phytoplankton biomass, measured as chlorophyll per unit area, integrated vertically through the photic zone of the lake) and  $R$  (refractory DOC). Algal growth depends on a maximum growth rate  $r$ , self-shading through the logistic term  $[1 - (A/u)]$ , and shading by DOC through the hyperbolic term  $[s/(s + R)]$ . The maximum attainable phytoplankton biomass, if losses and RDOC are zero, is  $u$ . The DOC concentration at which shading reduces algal growth to half the maximal rate is  $s$ . Phytoplankton are lost to sinking and grazing at per-capita rate  $l$ . Refractory DOC dynamics depend on an input rate  $I$ , losses to photodegradation and other physical-chemical processes with rate constant  $p$ , and biological degradation (bracketed expression in eq. 6). Biological degradation is proportional to  $A$  because phytoplankton are assumed to be the major source of labile DOC. The rate constant for biological degradation is  $c$ . The sigmoid term  $h^2/(h^2 + R^2)$  represents the inhibitory effects of pH on cometabolism. The DOC level at which pH reduces biological degradation to half the maximum rate is  $h$ . Stability analysis of the model is explained in the Appendix.

Isoclines of eqs 6 and 7 are

$$A^* = (I - pR)(R^2 + h^2)/(cRh^2) \quad (8)$$

and

$$R^* = -s[rA + u(l - r)]/(lu) \quad (9)$$

These isoclines can have one intersection (a stable point) or three intersections (2 stable points and an unstable point). The number of intersections depends on the parameter values. Consequently eutrophy and dystrophy are alternative states of the system for cer-

tain parameter values (Fig. 2). At low input rates of RDOC, the system is eutrophic: chlorophyll levels are high and RDOC levels are low (Fig. 2A, C). Increasing RDOC input rates lead to a system with three equilibria: a stable eutrophic (high chlorophyll, low RDOC) state, an unstable intermediate state, and a stable dystrophic (low chlorophyll, high RDOC) state. At still higher RDOC input rates, the system is strongly dystrophic: chlorophyll levels are low, and RDOC levels are high. Similar state transitions occur as maximum algal biomass increases, as might occur if nutrient inputs to the lake increased (Fig. 2B, D). At low levels of the maximum algal biomass, the system is dystrophic. At intermediate levels of the maximum algal biomass, three equilibria occur: a stable eutrophic (high chlorophyll, low RDOC) state, an unstable intermediate state, and a stable dystrophic (low chlorophyll, high RDOC) state. At higher levels of the maximum algal biomass, the system is eutrophic.

### Parameter estimates for the mechanistic model

The literature yields ranges of parameters that probably represent most of the world's lakes (Table 1). Only  $c$ , the biological degradation coefficient, and  $h$ , the RDOC concentration that reduces microbial metabolism by half, are poorly represented in the literature.

For  $c$ , the minimal estimate is 0. We estimated the upper bound for  $c$  as follows. The yield of labile DOC from phytoplankton is variable, but a typical value is 5% of phytoplankton carbon per day (Björnsen 1988). Labile DOC is consumed by bacteria almost as fast as it is produced (Billen et al. 1990). If degradation of RDOC occurs at a 1:1 ratio with metabolism of labile DOC, then the upper bound for  $c$  is 0.05. However,

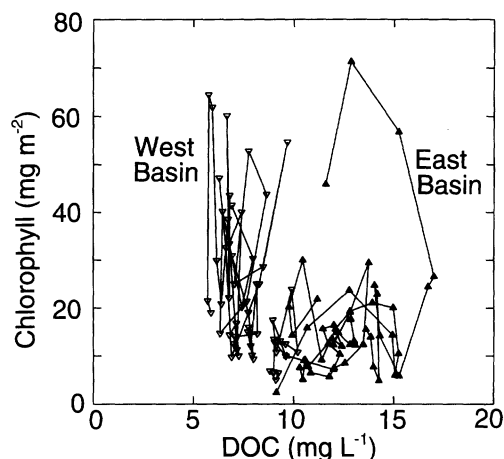


Fig. 3. Plots of integrated chlorophyll (mg m<sup>-2</sup>) versus DOC (mg L<sup>-1</sup>) in the West (open symbols) and East (closed symbols) of Long Lake during the summer stratified seasons of 1991-1994. For each basin, consecutive points within a season are connected by lines.

Table 1. Ranges of parameter values estimated from the literature. See text for further explanation.

Parameter and units	Values	Reference
$r$ , $d^{-1}$	0.1–2.5	Reynolds 1984
$u$ , chl $mg\ m^{-2}$	7–300	Canfield and Bachman 1981
$s$ , DOC $mg\ L^{-1}$	1–14	Jackson and Hecky 1980, Jones 1992, Christensen et al. 1996
$l$ , $d^{-1}$	0.01–0.8	Reynolds 1984
$I$ , $mg\ L^{-1}\ d^{-1}$	0.005–0.6	Likens 1985, Schindler et al. 1992, Wetzel 1983
$p$ , $d^{-1}$	0.001–0.09	De Haan 1993, Mopper et al. 1991, Rasmussen et al. 1989
$c$ , $m^2\ mg^{-1}\ d^{-1}$	0–0.005	see text
$h$ , DOC $mg\ L^{-1}$	5–20	see text

most analyses suggest that less RDOC is metabolized than labile DOC, though this question is an active area of research (Kieber et al. 1989, Moran and Hodson 1990, Tranvik 1992, De Haan 1993). If RDOC and labile DOC are metabolized at a ratio of 1:10, then the upper bound for  $c$  is 0.005.

Even less information is available for  $h$ . In experimental lake acidifications, bacterial processes have been severely inhibited at pH 4.5 (Schindler 1991). Other experiments show little or no effects of pH on microbial activity (Bell and Tranvik 1993). We infer, however, that the pH corresponding to  $h$  is probably 5 to 5.5. The range of RDOC concentrations associated with this pH is broad. In simulations, we assumed that  $h$  could lie between RDOC concentrations of 5 and 20  $mg\ L^{-1}$ .

As an alternative to the literature estimates, we also estimated parameters from data for Long Lake. Since the data were collected at discrete intervals, eqs 5 and 6 were converted to difference equations to estimate parameters. Fits of the model were improved substantially by including P input rates and an index of grazing effects in the model. The modified versions of eqs 6 and 7 were:

$$(A_{t+1} - A_t)/\Delta t = rP_t A_t [1 - (A_t/u)] \times [s/(s + R_t)] - lZ_t A_t \quad (10)$$

$$(R_{t+1} - R_t)/\Delta t = I - pR_t - [cA_t R_t h^2 / (h^2 + R_t^2)] \quad (11)$$

The subscript denotes time that a sample was taken. The time step ( $\Delta t$ ) was the interval between samples (7 d).  $P_t$  and  $Z_t$  are time series of areal P input rate ( $mg\ m^{-2}\ d^{-1}$ ) and crustacean length (mm), respectively. The state variable time series are  $A_t$  (areal chl,  $mg\ m^{-2}$ ) and  $R_t$  (DOC concentration,  $mg\ L^{-1}$ ). Definitions of the parameters  $r$  and  $l$  now accommodate effects of P input rate and potential grazing loss. The maximum chlorophyll growth rate per unit P input rate is  $r$ . The chlorophyll loss rate per mm of mean crustacean length is  $l$ .

Eqs 10 and 11 were estimated in 3 parts to conform to the structure of the data. (1) Eq. 10 was fit to time

series of  $A$ ,  $R$ ,  $P$  and  $Z$  to estimate  $r$ ,  $u$ ,  $s$  and  $l$ . Parameter distributions were determined by bootstrapping (Efron and Tibshirani 1993). (2) The biological degradation term (bracketed expression in eq. 11) was fit to the respiration time series to estimate  $c$  and  $h$ . Parameter distributions were determined by bootstrapping. Conversion from oxygen to carbon assumed a molar respiratory quotient of unity. (3) Eq. 11 was fit to weekly time series of  $R$  and  $A$  to estimate  $I$  and  $p$ , after fixing  $c$  and  $h$  to the optimal values estimated in step 2. Since the resulting equation is linear in  $I$  and  $p$ , their variances and covariance were estimated by ordinary least squares. This two-stage fit of eq. 11 was necessary because fits to DOC time series alone cannot discriminate biological degradation ( $c$ ) from other losses of DOC ( $p$ ).

## Results

### Regression tests for alternative states

A phase plot of chlorophyll and DOC from Long Lake suggests that the two basins may have different attractors (Fig. 3). However, this visual impression is not well supported by statistical analyses reported below. More likely, the interbasin difference is caused by sustained differences in RDOC input (Christensen et al. 1996).

Bayesian estimates of the probability of alternative stable states were 0.541 for the DOC time series and 0.528 for the chlorophyll time series. This result is equivocal. It suggests that a single stable state is about as likely as alternative stable states.

The DOC time series was fit equally well by the two polynomial models (likelihood ratio = 1.008). The DOC data also fit both autoregressive models equally well (likelihood ratio 0.974; extra sum of squares test  $F_{2,5} = 0.006$ ). These results are equivocal. Models with one or two stable states are equally likely to fit the data.

The chlorophyll time series fit eq. 2 slightly better than eq. 3 (likelihood ratio = 1.42). This result suggests that a model with one stable state is slightly more likely to fit the data than a model with two stable states.

Table 2. Parameter estimates and standard deviations for fits of difference equations to data from East and West Long lakes, 1991–1994. Bootstrap statistics are based on 1000 iterations.

Parameter and units	Value	<i>s</i>	Bootstrap stats	
			mean	median
<i>r</i> , m <sup>2</sup> mg <sup>-1</sup>	0.223	0.869	0.779	0.359
<i>u</i> , chl mg m <sup>-2</sup>	54.2	6.5	52.1	52.7
<i>s</i> , DOC mg L <sup>-1</sup>	1.54	21.27	9.56	0.79
<i>l</i> , d <sup>-1</sup> mm <sup>-1</sup>	0.0467	0.0231	0.0315	0.0311
<i>I</i> , DOC mg L <sup>-1</sup> d <sup>-1</sup>	0.0122	0.0035	–	–
<i>p</i> , d <sup>-1</sup>	5.61E–2	3.38E–2	–	–
<i>c</i> , m <sup>2</sup> mg <sup>-1</sup> d <sup>-1</sup>	7.14E–4	1.06E–5	9.29E–4	0.919E–4
<i>h</i> , DOC mg L <sup>-1</sup>	27.5	16.2	27.5	23.6

However, the DOC time series gave the opposite result. Eq. 4 fits slightly better than eq. 5 (likelihood ratio 2.53; extra sum of squares test  $F_{2,5} = 0.93$ ), implying that a model with two states is slightly more likely to fit the data than a model with one state. In view of two opposing results, both of them weak, we conclude that the result is equivocal. The tests provide no strong evidence for or against alternative states of the ecosystem.

### Mechanistic model: parameters from the literature

We analyzed 100 000 parameter sets drawn randomly from uniform distributions with the ranges estimated from the literature (Table 1) to assess the probability of alternative stable states. Stability analysis followed the procedure shown in the Appendix. 60.5% of the parameter sets produced only one positive stable point. 31.2% of the parameter sets had no positive equilibria. For 8.2% of the parameter sets, there was one positive stable point and one positive unstable point. In all of these cases, the second attractor had negative algal biomass implying a completely dystrophic lake. We count these as examples of alternative stable states. Only 0.1% of the parameter sets yielded three positive equilibria, two stable and one unstable. This result suggests that alternative states of eutrophy and dystrophy are relatively uncommon, occurring in only 8.3% of the cases examined.

Conditions leading to alternative states were complex and no strong, simple patterns emerged. There was a weak tendency for alternative states to be more common at high values of *I* (the input rate of RDOC) or at high values of *u* (the maximum algal biomass).

### Mechanistic model: fits to Long Lake data

Eqs 10 and 11 fit the chlorophyll and DOC time series well (Fig. 4). The residuals are approximately normally distributed, have no significant autocorrelations, and no significant cross-correlations with predictor time series. Although a substantial amount of variance in

chlorophyll is not explained by the model, there is no pattern in the residuals that suggests the model can be improved.

Parameter estimates and uncertainties are collected in Table 2. Estimates of *u*, *l*, *I*, *c*, and *p* are large relative to their standard deviations. Estimates of *r* and *s* have relatively large standard deviations. However, *r* and *s* have a large negative covariance (Fig. 5), so variations in *r* and *s* have compensatory effects on predictions of algal dynamics. Consequently predictions based on the joint distribution of *r* and *s* have only a moderate variance (Fig. 4). The joint distribution of *c* and *h* also has a large negative covariance (Fig. 5) leading to modest variability in predictions of DOC (Fig. 4).

To assess the probability of alternative states, we analyzed 100 000 parameter sets drawn randomly from the joint distribution of *r*, *u*, *s* and *l*, the joint distribution of *c* and *h*, and the joint distribution of *I* and *p*. *P<sub>t</sub>* and *Z<sub>t</sub>* were drawn from their observed distribution in Long Lake. Stability analysis followed the procedure shown in the Appendix, except that we substituted *rP* for *r*, and *lZ* for *l*. Only 7.7% of the parameter sets had no positive equilibria. 78.7% of the parameter sets produced only one positive stable point. For 13.4% of the parameter sets, there was one positive stable point and one positive unstable point. In all of these cases, the other attractor had negative algal biomass implying a completely dystrophic lake. We count these as exam-

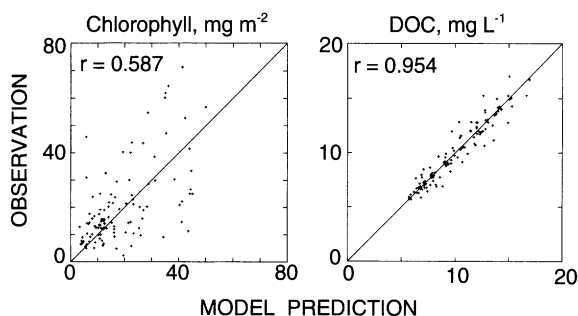


Fig. 4. Scatterplots of observations versus model predictions for (left panel) areal chlorophyll and (right panel) DOC in Long Lake. Solid line shows where observations and predictions are identical.

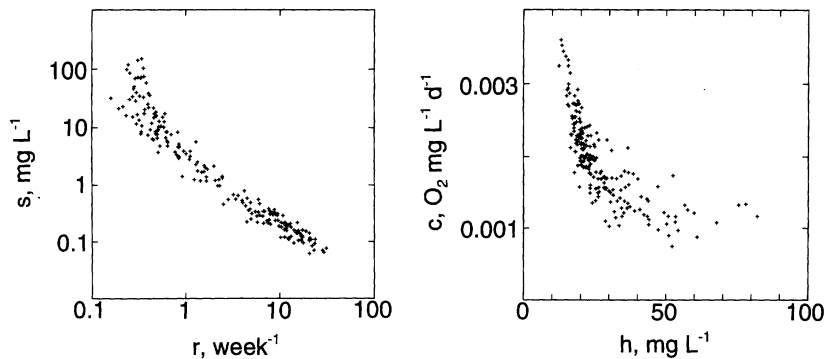


Fig. 5. Scatterplots of bootstrap estimates of (left panel)  $s$  and  $r$ , and (right panel)  $c$  and  $h$ .

ples of alternative stable states. Only 0.2% of the parameter sets yielded three positive equilibria, two stable and one unstable. Like the literature evaluation, our parameter estimates from Long Lake data suggest that alternative stable states of eutrophy and dystrophy are not common, occurring in only 13.6% of the cases examined.

### Mechanistic model: return time and simulations

We calculated ecosystem return time for the Long Lake model as  $-1/\lambda_{m,r}$  where  $\lambda_{m,r}$  is the real part of the maximum eigenvalue of the Jacobian matrix (Appendix). Thus defined, the return time is the time required for a perturbation away from a stable point to decay by a factor of  $1/e$  where  $e$  is the base of natural logarithms. For all stable points that arose from the parameter distributions, the mean return time is 316 d (standard deviation = 108 d). This return time is comparable to Long Lake's hydraulic residence time, approximately 100 to 500 d (Carpenter et al. 1996). It is longer than the return time of the P cycle derived from a model of the foodweb of Tuesday Lake (28–204 d), a nearby, similar ecosystem (Carpenter et al. 1992a, b). Our estimate of the return time for the chlorophyll–RDOC system is based on rates measured during summer stratification, which are faster than annual averages. Consequently, our data probably underestimate the true return time.

The rate of change of Long Lake is so slow that important perturbations are likely to occur before a stable point is reached. Major inputs of P and RDOC to Long Lake occur with spring snowmelt and precipitation which vary substantially from year to year. Substantial changes in grazing rate during fish recruitment events can be expected every few years (Carpenter and Kitchell 1993). Perturbations of inputs and fluctuations in the food web may be so frequent that the ecosystem does not reach steady state in chlorophyll and RDOC. This prospect shifts our focus from the distribution of steady states to the distribution of ecosystem states at some time following a disturbance. We first considered

the ecosystem states resulting after 100 d under contrasting regimes of grazing, P input, and RDOC input. We then also considered ecosystem recovery from pulsed inputs of P and RDOC.

Trajectories of Long Lake were simulated for eight scenarios resulting from low or high levels of three factors: grazing losses (mean crustacean length = 0.2 or 1.2 mm), P input rate (0.5 or 5.0  $\text{mg m}^{-3} \text{d}^{-1}$ ), and RDOC input rates (0.01 or 0.1  $\text{g m}^{-3} \text{d}^{-1}$ ). 100 simulations of a summer stratified season were run for each scenario. For each simulation, parameters were drawn randomly from the joint distribution of  $r$ ,  $u$ ,  $s$  and  $l$ , the joint distribution of  $c$  and  $h$ , and the distribution of  $p$ . Initial conditions were the long-term mean chlorophyll and DOC observed in Long Lake. Bivariate 90% confidence ellipses were calculated for the final day (day 100) of the simulations for each scenario.

The simulations revealed substantial dynamic variability (Fig. 6). Variability in chlorophyll was greater than variability in RDOC. The overlapping distributions of chlorophyll concentrations do not suggest distinctly different ecosystem states. Rather, they suggest a continuum of trophic conditions. The tenfold range in RDOC input rates produced distinctly different distributions of RDOC concentration that field workers would recognize as very different ecosystem states. However, these are not necessarily alternative stable

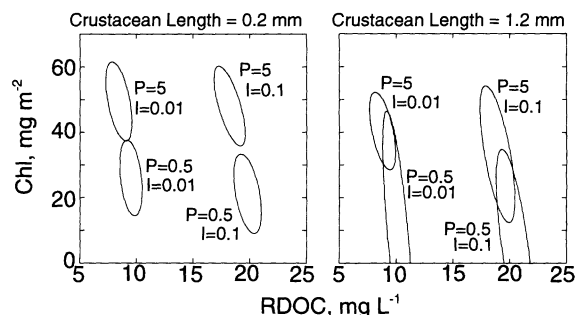


Fig. 6. Plots of areal chlorophyll versus RDOC for stochastic dynamic simulations of Long Lake. Each ellipse is a 90% bivariate confidence region for 100 simulations with a fixed crustacean length, phosphorus input rate, and RDOC input rate.

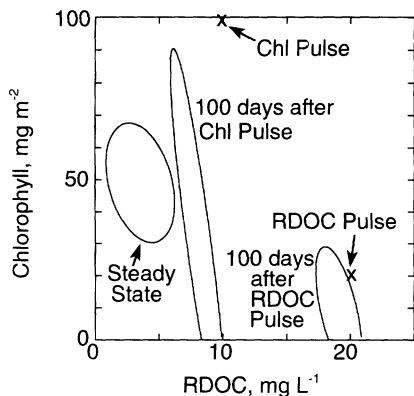


Fig. 7. Plots of areal chlorophyll versus RDOC for steady state conditions and simulations of a chlorophyll pulse (as could result from a large pulse of P input) and a RDOC pulse. Each ellipse is a 90% bivariate confidence region for 100 simulations with crustacean length and phosphorus input rate fixed at the mean for Long Lake.

states. They are caused by different input rates of RDOC, and maintained by slow dynamics of RDOC.

A substantial pulse of RDOC into a lake could have relatively long-lasting effects. We compared the dynamics of a P pulse that increased chlorophyll levels to twice the long-term mean in Long Lake, and a RDOC pulse that increased RDOC to twice the long-term mean (Fig. 7). After a 100-d summer stratified season, the chlorophyll pulse decayed to nearly the steady-state level, although variability was relatively high. The RDOC pulse scarcely decayed in 100 d. Phosphorus pulses to lakes are rapidly assimilated by the food web or sedimented, at rates that are typically much faster than flushing of the lake (Schindler 1977, 1991, Carpenter et al. 1992a, b). RDOC pulses decay through photodegradation, metabolism, and flushing, processes with similar rates in Long Lake. Relatively slow losses of RDOC are known from other systems as well (Jones 1992, Schindler et al. 1992). Thus refractory DOC is a relatively slow compartment that acts as a constraint on chlorophyll.

## Discussion

In view of the long-standing importance of the alternative states concept in ecology (Holling 1973), it is surprising that methods for assessing alternative states in ecosystem data are not well developed. We expect that further work on this problem will lead to better statistical approaches than those we have used. Because the literature offers no clear guidelines, we used several very different approaches in this study. In this case, diverse analyses yielded similar conclusions.

Our results do not offer strong support for the idea that *internal* processes in lakes can maintain alternative states of eutrophy and dystrophy. A landscape perspec-

tive is necessary to understand the processes that maintain dystrophic or eutrophic states, and sometimes cause lakes to change state. Alternative states of eutrophy and dystrophy depend on relatively slow processes of landscape change, relatively rapid cycling of P in the plankton, and processes with intermediate rates such as fish recruitment (Carpenter and Kitchell 1993) and RDOC dynamics. The interaction of these processes is sometimes stabilizing, but under certain conditions changes in P or RDOC inputs or in the food web cause rapid shifts in ecosystem state. Perturbations of inputs and food web structure may be frequent enough that chlorophyll and RDOC are always far from steady state. If so, it is more productive to study the dynamic variability rather than behavior near presumed steady states.

This study is certainly not the last word on whether eutrophy and dystrophy are alternative stable states. Our simulations show that alternative states occur for roughly 10% of feasible parameter sets, and therefore probably occur for many lakes at one time or another. Input rate of RDOC is a critical driver. Strong tests of the alternative state hypothesis could be made by adding more RDOC to a lake, or by comparisons of lakes across a gradient of RDOC input. As to mechanisms, two crucial feedbacks between chlorophyll and RDOC in lakes are shading and biological degradation. The former is well known (Jones 1992). The latter is not, and should be a focus of research to better understand transitions between eutrophy and dystrophy.

Our analysis has focused on selected lake processes, specifically the interaction of DOC inputs with P inputs and food web structure. We have not considered other factors which may affect stability of lake trophic states or induce alternating trophic states. For example, sustained P inputs which build up P-rich sediments may lead to effective internal cycling which stabilizes a eutrophic condition (National Research Council 1992). Massive RDOC inputs may lower pH and thereby change the fish community and food web structure for extended periods of time (Tonn and Magnuson 1982). Grazer-phytoplankton interactions may assume alternative stable states (Scheffer 1991). In shallow lakes, macrophyte dominance and phytoplankton dominance are classic examples alternative stable states (Scheffer et al. 1993). These examples suggest that alternative stable states may be an appropriate model for several aspects of lake ecosystems.

Landscape processes are important factors in the regional distribution of dystrophic and eutrophic lakes. The role of agriculture and urbanization in eutrophication of lakes is well known (National Research Council 1992). Phosphorus inputs are a principal driver (Schindler 1977). Loss of wetlands may exacerbate eutrophication by reducing RDOC inputs to lakes, and reducing the capacity of the landscape to hold water and nutrients (Wetzel 1990). Conversion of wetlands for agricul-

ture and other uses is common. For example, the United States (excluding Alaska) has lost 53% of its wetlands since the 1780s, an area of about 49 million ha (Dahl 1990). Wetland loss intensifies flooding and increases nutrient flow from land to water (National Research Council 1992). Also, wetlands are a major source of RDOC to lakes (Kortelainen 1993, Driscoll et al. 1994). Responses of chlorophyll to P inputs and symptoms of eutrophication increase as RDOC inputs to lakes decrease.

Climate-induced hydrologic fluctuations have potentially large effects on lake trophic state. Our analysis suggests that transitions between eutrophy and dystrophy are reversible, but dynamics may be slow. Large RDOC pulses, which may occur when wetlands are temporarily flooded, disappear relatively slowly. High RDOC levels work synergistically with high levels of large grazers to suppress responses of algae to P inputs. Droughts, which reduce RDOC inputs, lead to low RDOC levels as standing stocks are degraded, thereby increasing the sensitivity of the ecosystem to changes in P input, P recycling or grazing (Schindler et al. 1990).

A changing climate is likely to shift the relative frequencies of oligotrophic, dystrophic, and eutrophic lakes on the landscape. Climate effects will interact with direct effects of humans on landscape vegetation and lake communities. Intensification of agriculture and urbanization increase P inputs to lakes (National Research Council 1992). Conversion of wetlands will reduce RDOC inputs to lakes and increase the sensitivity of phytoplankton biomass to fluctuations in P input and food web structure. Fishing exacerbates fluctuations in food web structure and increases variability in phytoplankton biomass (Kitchell and Carpenter 1993). These direct effects of humans on lakes are far more certain than effects of climate change. Although effects of climate change are uncertain, climate has powerful interactions with direct effects of humans on lakes. These interactions will probably determine the trophic states of the world's lakes in the next century.

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## Appendix. Stability analysis

Stability analyses followed the standard approach described in many ecology textbooks (DeAngelis 1992). By definition the stable points of eqs 6 and 7 are obtained by setting the equations equal to 0 and solving for  $A$  and  $R$ . This leads to a cubic polynomial in  $R_*$ , the equilibrium value of  $R$ :

$$0 = -prsR_*^3 + (ch^2lu + Irs)R_*^2 + h^2s(cu(l-r) - pr)R_* + h^2Irs \quad (A1)$$

Eq. A1 will have either 1 real root and 2 complex roots for  $R_*$ , or 3 real roots for  $R_*$ . Real values of  $R_*$  are then used to solve for  $A_*$ , the real equilibrium value of  $A$ :

$$A_* = u[R_*l + s(l-r)]/(sr) \quad (A2)$$

We now have 1 or more combinations of real  $A_*$  and  $R_*$  values at which  $dA/dt = dR/dt = 0$ . The Jacobian matrix  $\mathbf{J}$  is used to check the stability of any one of these combinations. The top row of  $\mathbf{J}$  is the derivatives of the right hand side of eq. 6 with respect to  $A$  and  $R$ . The bottom row of  $\mathbf{J}$  is the derivatives of the right hand side of eq. 7 with respect to  $A$  and  $R$ . The elements of  $\mathbf{J}$  are:

$$J_{1,1} = -\{2A_*rs + u[R_*l + s(l-r)]\}/[u(R_* + s)] \quad (A3)$$

$$J_{1,2} = A_*rs(A_* - u)/[u(R_* + s)^2] \quad (A4)$$

$$J_{2,1} = -cR_*h^2/(R_*^2 + h^2) \quad (A5)$$

$$J_{2,2} = [A_*ch^2(R_*^2 - h^2)/(R_*^2 + h^2)^2] - p \quad (A6)$$

Let  $\lambda_m$  be the eigenvalue of  $\mathbf{J}$  whose real part is the largest. If the real part,  $\lambda_{m,r}$  is positive, then the equilibrium point is unstable, or a repeller, and the system will move away from it. If  $\lambda_{m,r}$  is negative, then the equilibrium point is stable, or an attractor, and the system will move toward it. The rate of movement toward the attractor is proportional to  $\exp(-\lambda_{m,r})$ . A common definition of return time to the attractor following a modest perturbation is  $-1/\lambda_{m,r}$  (DeAngelis 1992).

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