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PREDICTIVE INDICES OF ECOSYSTEM RESILIENCE IN MODELS OF NORTH TEMPERATE LAKES¹

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Abstract. Predictive indicators of the rate of ecosystem recovery after a perturbation (resilience) could be valuable tools for ecological studies that need to anticipate system response to perturbation. We used a simulation model of summer phosphorus cycling in north temperate lakes to (1) evaluate whether resilience decreases with increasing food web length and increases with increasing nutrient loading and (2) test the correspondence between two potential indicators of resilience (nutrient turnover rate, NTR, and the dominant eigenvalue, λ_{\max}) and postperturbation measurements of recovery rate. We determined λ_{\max} and NTR for reference simulations of planktivore- and piscivore-dominated food webs at three baseline phosphorus loading rates (0.1, 1.0, and 2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$), then measured recovery rates from simulated pulses of available phosphorus. The planktivore-dominated (short) food web was more resilient at baseline phosphorus loading rates of 0.1 and 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$. However, the piscivore-dominated (long) food web was more resilient at the highest baseline phosphorus loading rate (2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$), apparently because the additional nutrients were incorporated into biota more rapidly. Recovery rates predicted from NTR (but not from λ_{\max}) were consistent with measured recovery rates. NTR appears to be a useful predictor of lake ecosystem recovery from nutrient pulses, particularly because it can be estimated relatively easily. Field tests comparing preperturbation estimates of NTR and postperturbation recovery rates are necessary to further validate this approach.

Key words: ecosystem; eigenvalue; food web; lake; nutrient loading; nutrient turnover rate; phosphorus cycling; pulse perturbations; resilience; simulation model.

INTRODUCTION

Predicting the rate at which an ecosystem might rebound from perturbation is crucial for ecological assessment, impact, and restoration studies. Resilience, the rate of recovery to the predisturbance state (Webster et al. 1975, Pimm 1984, 1991, DeAngelis et al. 1989a, b, DeAngelis 1992), is an established ecological concept germane to this issue. Ecosystem resilience is thought to increase with increasing nutrient loading rate (DeAngelis et al. 1989a) and decrease with increasing food chain length (Pimm and Lawton 1977). However, interactions among these factors are not straightforward (DeAngelis et al. 1989a). This complexity makes it difficult to make predictions about the relative resilience of different systems based on static nutrient and food web characteristics.

However, it may be possible to anticipate resilience using indices based on dynamic characteristics of ecosystems. The extensive literature on resilience (e.g., Harwell et al. 1977, 1981, Bloom 1980, DeAngelis 1980, 1992, Pimm 1982, 1984, 1991, DeAngelis et al. 1989a, 1990, Steinman et al. 1991, 1992, Carpenter et al. 1992) suggests two potential predictors: (1) the dominant eigenvalue (λ_{\max}) of a linear model of the system and (2) the nutrient turnover rate of the system, NTR. Both can be estimated before perturbation, although NTR may be easier to estimate than λ_{\max} .

Direct measurements of recovery rate and preperturbation estimates of NTR and λ_{\max} have not yet been compared in a systematic way for different types of perturbations. Field tests will be difficult and expensive. Ecosystem models, though, provide the flexibility needed to compare indices and measures for many different perturbations and may suggest critical field tests. In this study, we use a simulation approach to evaluate questions about resilience.

Lakes are excellent systems in which to evaluate ecosystem response to perturbation (Schindler 1990). In this paper, we focus on north temperate lake ecosystems where responses to changes in nutrients (Schindler 1988, Edmondson 1991, Kitchell 1992) and pelagic food webs (Kerfoot and Sih 1987, Carpenter 1988, Kitchell 1992, Carpenter and Kitchell 1993) are relatively well understood. Our simulation model incorporates nonlinearities of lake ecosystems, such as predator-prey interactions (Brooks and Dodson 1965, Kerfoot and Sih 1987) and nutrient recycling by consumers (Kitchell et al. 1979, Carpenter et al. 1992, Schindler et al. 1993), which can influence ecosystem responses to perturbation.

We explore differences in model response to pulse perturbations of phosphorus loading under two contrasting food web structures and three baseline phosphorus loading rates. We first reconsider the hypothesized relationships between resilience, nutrient loading, and food web length using measurements of resilience calculated from perturbed simulations. Then we ex-

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amine the consistency of the predictive indices (λ_{\max} and NTR, calculated from reference simulations) with measured recovery rates.

METHODS

Model description

Our nonlinear model simulates phosphorus cycling among pelagic biota in a vertically stratified temperate lake during the summer (Fig. 1; Cottingham 1993). Thermal stratification separates many temperate lakes into three strata: the epilimnion, metalimnion, and hypolimnion. Nutrient levels are generally low in the epilimnion but increase with depth (Wetzel 1983). Maximum algal biomass occurs in either the epilimnion or metalimnion, depending on water transparency and amount of primary production (Moll and Stoermer 1982). When light levels are sufficient for algal growth, metalimnetic populations exploit the high nutrient levels at the thermocline, creating discontinuous profiles of chlorophyll with depth. However, with increasing nutrient input to the epilimnion, epilimnetic algal populations may become large enough to decrease light levels reaching the metalimnion, shading out metalimnetic algae (Moll and Stoermer 1982). The model allows this possibility.

Size-structured interactions are important to lake predator-prey relationships (Kerfoot and Sih 1987). Our model incorporates size-based distinctions by dividing algae and zooplankton into small and large compartments and by including diel vertical migrations of organisms vulnerable to visual predation. Algal vulnerability to zooplankton grazing depends on cell size and on zooplankton size (Burns 1969, Reynolds 1983). Larger zooplankton, especially *Daphnia* spp., consume larger algae, although some algae are large enough to escape predation altogether (Porter 1977). Small zooplankton are vulnerable to invertebrate predators such as *Chaoborus* spp. (Dodson 1972, Neill 1981), while large zooplankton (including *Chaoborus*) are more vulnerable to visually feeding zooplanktivorous fishes (Brooks and Dodson 1965). In many lakes, large zooplankton and invertebrate planktivores avoid the epilimnion during the day and migrate upwards from the metalimnion and hypolimnion during the night. These migrations are due at least in part to avoidance of fish predation (Lampert 1989, Dini and Carpenter 1991, 1992) and affect predation and recycling rates on daily time scales (Schindler et al. 1993).

Model structure is summarized in Fig. 1. Phosphorus enters the epilimnion via external inputs and metalimnetic entrainment; however, when external nutrient loading is low, nutrient recycling by consumers supplies much of the phosphorus available to primary producers (Kitchell et al. 1979, Schindler et al. 1993). Epilimnetic phosphorus is taken up by small and large algae, which sink to lower strata or are eaten by zooplankton. Consumers assimilate, excrete, or egest

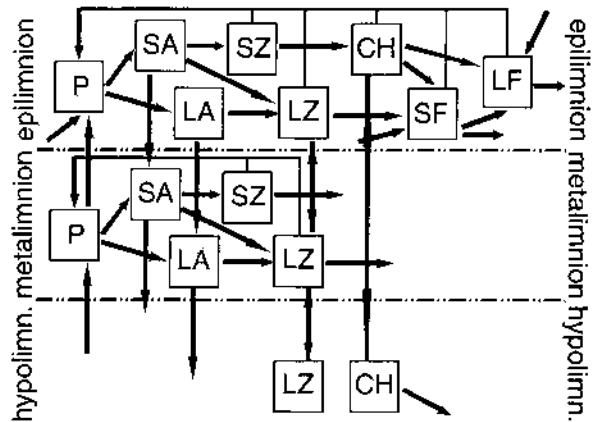


FIG. 1. State variables and links for our nonlinear deterministic simulation model. Arrows denote direct flows of phosphorus. Compartment sizes are measured as phosphorus concentrations ($\mu\text{g/L}$), and transfers between compartments are expressed as phosphorus concentration per day ($\mu\text{g} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$). The epilimnion and metalimnion each have compartments for available phosphorus (P), small algae (SA), large algae (LA), and small nonmigratory zooplankton (SZ). Large zooplankton (LZ) divide time evenly between the epilimnion and metalimnion, while *Chaoborus* (CH) spend 60% of each day in the hypolimnion and 40% in the epilimnion. Planktivorous (SF) and piscivorous (LF) fish are restricted to the epilimnion.

phosphorus they ingest (egestion is not shown in Fig. 1).

Algal growth (Γ) was mediated by temperature, light, and phosphorus concentration:

$$\Gamma = V_{\max} \cdot f(T) \cdot [\min\{f(L), f(P)\}]. \quad (1)$$

V_{\max} represents the maximum potential growth rate. The light limitation function $f(L)$ accounted for self-shading of algae and nutrient limitation $f(P)$ was modeled with a Michaelis-Menten function. The temperature function $f(T)$ scaled growth from 0 to 1, with increases up to the optimal temperature and decreases above it (Kitchell et al. 1974).

Predator-prey interactions were mediated through a functional response that allows for interference competition among predators (DeAngelis et al. 1975) and selectivity among multiple prey categories (O'Neill 1969, 1976, Bartell et al. 1988, DeAngelis et al. 1989a). Predation on prey compartment i by predator j ($\Pi_{i,j}$) was modeled as:

$$\Pi_{i,j} = C_{\max} \cdot f(T) \cdot \left\{ \frac{w_{i,j} B_i B_j}{B_j + \sum_{k=1}^n (w_{k,j} B_k)} \right\}, \quad (2)$$

where C_{\max} is the maximum potential consumption rate for predator j , $f(T)$ is the temperature function for predator j , $w_{i,j}$ is the selectivity of predator j for prey i , B is the amount of phosphorus in a compartment, k is the index over prey types, and n is the number of prey types consumed by predator j .

Dynamics of all state variables were described by

TABLE 1. Equations for state variable dynamics. Detailed explanations are in Cottingham (1993).

State variables	Equation	State variables	Equation
Epilimnetic phosphorus (P_E)	$\frac{dP_E}{dt} = (I + E_M + U) - (\Gamma_{A_E} + \Gamma_{B_E} + f)$	$\Pi_{B_M,Z}$	= predation on metalimnetic large algae by migratory large zooplankton
	I = external P input	Epilimnetic small zooplankton (Z_E)	$\frac{dZ_E}{dt} = Z_E(a_{A_E,Z_E} \Pi_{A_E,Z_E} - \Pi_{Z_E,C})$
	E_M = entrainment from the metalimnion		a_{A_E,Z_E} = assimilation efficiency for small zooplankton feeding on small algae
	U = excretion from all biotic compartments currently feeding in the epilimnion; depends on values of $\Pi_{i,j}$		$\Pi_{Z_E,C}$ = predation on small zooplankton by <i>Chaoborus</i>
	Γ_{A_E} = uptake by epilimnetic small algae (Eq. 1)	Metalimnetic small zooplankton (Z_M)	$\frac{dZ_M}{dt} = Z_M(a_{A_M,Z_M} \Pi_{A_M,Z_M} - D_{Z_M})$
	Γ_{B_E} = uptake by epilimnetic large algae		a_{A_M,Z_M} = assimilation efficiency for small zooplankton feeding on small algae
	f = flushing rate		D_{Z_M} = death rate of metalimnetic small zooplankton
Metalimnetic phosphorus (P_M)	$\frac{dP_M}{dt} = (I + E_H + U) - (E_M + \Gamma_{A_M} + \Gamma_{B_M} + f)$	Large zooplankton (Z) in the epilimnion	$\frac{dZ}{dt} = Z(a_{A,Z} \Pi_{A,Z} + a_{B,Z} \Pi_{B,Z} - \Pi_{Z,F})$
	E_H = entrainment from the hypolimnion		$a_{A,Z}$ = assimilation efficiency for large zooplankton feeding on small algae
	Γ_{A_M} = uptake by metalimnetic small algae		$a_{B,Z}$ = assimilation efficiency for large zooplankton feeding on large algae
	Γ_{B_M} = uptake by metalimnetic large algae	Large zooplankton (Z) in the metalimnion	$\frac{dZ}{dt} = Z(a_{A,Z} \Pi_{A,Z} + a_{B,Z} \Pi_{B,Z} - D_Z)$
Epilimnetic small algae (A_E)	$\frac{dA_E}{dt} = A_E(\Gamma_{A_E} - S_{A_E} - \Pi_{A_E,Z_E} - \Pi_{A_E,Z})$		$a_{A,Z}$ = assimilation efficiency for large zooplankton feeding on small algae
	S_{A_E} = sinking rate for epilimnetic small algae		$a_{B,Z}$ = assimilation efficiency for large zooplankton feeding on large algae
	Π_{A_E,Z_E} = predation on epilimnetic small algae by epilimnetic small zooplankton (Eq. 2)		D_Z = death rate of large zooplankton
	$\Pi_{A_E,Z}$ = predation on epilimnetic small algae by migratory large zooplankton	<i>Chaoborus</i> (C)	$\frac{dC}{dt} = C(a_{Z,E,C} \Pi_{Z,E,C} - \Pi_{C,F_2} - \Pi_{C,F_1})$
Metalimnetic small algae (A_M)	$\frac{dA_M}{dt} = A_M(\Gamma_{A_M} + S_{A_E} - S_{A_M} - \Pi_{A_M,Z_M} - \Pi_{A_M,Z})$		$a_{Z,E,C}$ = assimilation efficiency for <i>Chaoborus</i> feeding on epilimnetic small zooplankton
	S_{A_M} = sinking rate for metalimnetic small algae		Π_{C,F_2} = predation on <i>Chaoborus</i> by small fish
	Π_{A_M,Z_M} = predation on metalimnetic small algae by metalimnetic small zooplankton		Π_{C,F_1} = predation on <i>Chaoborus</i> by large fish
	$\Pi_{A_M,Z}$ = predation on metalimnetic small algae by metalimnetic large zooplankton	Small fish (F_s)	$\frac{dF_s}{dt} = F_s(G_s - D_s)$
Epilimnetic large algae (B_E)	$\frac{dB_E}{dt} = B_E(\Gamma_{B_E} - S_{B_E} - \Pi_{B_E,Z})$		G_s = small fish growth rate
	S_{B_E} = sinking rate for epilimnetic large algae		D_s = small fish death rate
	$\Pi_{B_E,Z}$ = predation on epilimnetic large algae by migratory large zooplankton	Large fish (F_l)	$\frac{dF_l}{dt} = F_l(G_l - D_l)$
Metalimnetic large algae (B_M)	$\frac{dB_M}{dt} = B_M(\Gamma_{B_M} + S_{B_E} - S_{B_M} - \Pi_{B_M,Z})$		G_l = large fish growth rate
	S_{B_M} = sinking rate for metalimnetic small algae		D_l = large fish death rate

differential equations (Table 1) solved numerically with fourth-order Runge-Kutta integration (Press et al. 1984) using 100 time-steps per day. Surface irradiance changed daily, and temperature and thermocline depth changed weekly. All simulations were run for 16 wk. A full description of model structure, equations, parameters, and sensitivity analysis appears in Cottingham (1993).²

We calibrated the model to two contrasting food web configurations: one dominated by planktivorous fish and one dominated by piscivorous fish. These food webs represent extreme contrasts for lakes with fish (Carpenter and Kitchell 1993). Calibration data came from planktivore-dominated Peter and piscivore-dominated Paul lakes at the University of Notre Dame Environmental Research Center near Land O'Lakes, Wisconsin. These are small, steep-sided lakes with minimal littoral zone development (Carpenter and Kitchell 1993) and high metalimnetic algal biomass (St. Amand and Carpenter 1993). Paul Lake has served as a control lake for ecosystem experimentation since 1951 and the fish community has been dominated by piscivorous largemouth bass since 1978 (Carpenter and Kitchell 1993). The food web of Peter Lake has often been manipulated, most recently in 1991 to establish a community dominated by planktivorous golden shiners (Schindler et al. 1993).

We simulated these contrasting food webs at three baseline phosphorus loading rates. The lowest level, $0.1 \mu\text{g} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$, corresponds to phosphorus loading rates estimated to occur in Peter and Paul lakes (Carpenter 1992). The highest level, $2.0 \mu\text{g} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$, is within the range observed for many eutrophic lakes (Vollenweider 1968). The intermediate level, $1.0 \mu\text{g} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$, may be near a boundary that separates trophic state in lakes (Benndorf 1990, Persson et al. 1992).

The model reproduced summer dynamics similar to those observed in lakes that span a range of food web configurations and nutrient loading rates. Increases in daily phosphorus loading rates caused increases in mean chlorophyll concentration within the range predicted from empirical regressions. Simulations at $0.1 \mu\text{g} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ baseline phosphorus loading generally were within 1 SD of the seasonal dynamics in Peter and Paul lakes. Details of the calibration and validation of the model will be addressed in a separate publication.

Before calculating resilience indices and measures, we simplified model output by combining functionally similar compartments (those that differed only in lake stratum or size) into trophic levels. For example, the four algal compartments were aggregated by summing small and large compartments in the epilimnion and

metalimnion. The condensed piscivore-dominated food web had length = 6 (phosphorus, algae, zooplankton, *Chaoborus*, planktivorous fish, and piscivorous fish), while the planktivore-dominated food web had length = 5 (all but piscivorous fish). These groupings are typical of limnological sampling programs and facilitate comparison to analyses of real lakes (Carpenter et al. 1992, Persson et al. 1993).

Resilience indices

We evaluated two indices of resilience in reference simulations of the model: the dominant eigenvalue and nutrient turnover rate. Resilience is thought to be positively related to both of these indices (DeAngelis 1992).

The dominant eigenvalue, λ_{max} , is the eigenvalue closest to zero in the matrix of flux rates of a linearized model. When real parts of all eigenvalues are less than zero, the system equilibrium is stable (DeAngelis 1992). We estimated λ_{max} from a donor-controlled linear matrix model parameterized from time courses for each trophic level. Translation of the daily nonlinear model output to the linear system followed the framework and assumptions of Carpenter et al. (1992). λ_{max} may be difficult to calculate from field data because it requires extensive information about the system, including standing stocks and transfer rates for each component (Carpenter et al. 1992).

Nutrient turnover rate (NTR, the ratio of external nutrient flow to nutrient standing stock) is much simpler to estimate than λ_{max} , yet appears to yield comparable information about ecosystem recovery when nutrient input is the factor that limits recovery (Harwell et al. 1977, 1981, DeAngelis et al. 1989a, Carpenter et al. 1992, DeAngelis 1992). NTR integrates aspects of nutrient inputs and recycling and can be estimated directly from field data on nutrient input rate, nutrient output rate, and the total amount of nutrient in the system (Carpenter et al. 1992). We estimated NTR by calculating phosphorus input and output rates for the whole system, then dividing the average of these by the average system standing stock of phosphorus (Watson and Loucks 1979).

Whether λ_{max} or NTR more accurately predicted the resilience of this lake ecosystem model was evaluated by perturbing the simulation model and comparing return times estimated from λ_{max} and NTR with measured return times. We took the reciprocals of NTR and $-\lambda_{\text{max}}$ in order to estimate return times from λ_{max} and NTR.

Perturbations and measurements of recovery

We ran 10 simulations of each of the six combinations of food web structure and baseline phosphorus loading rate under perturbed conditions. Each perturbation was a single pulse of nutrients into the epilimnetic available phosphorus compartment on day 50 of the simulation. The 10 different pulse perturbations

² See ESA Supplementary Publication Service Document Number 9401 for a copy of the computer code used for results shown here. This document is available on 5 1/4" diskette or in printed form. For a copy of this document, contact the (senior) author or order from the Ecological Society of America, 328 East State Street, Ithaca, NY 14850-4318 USA. There is a small fee for this service.

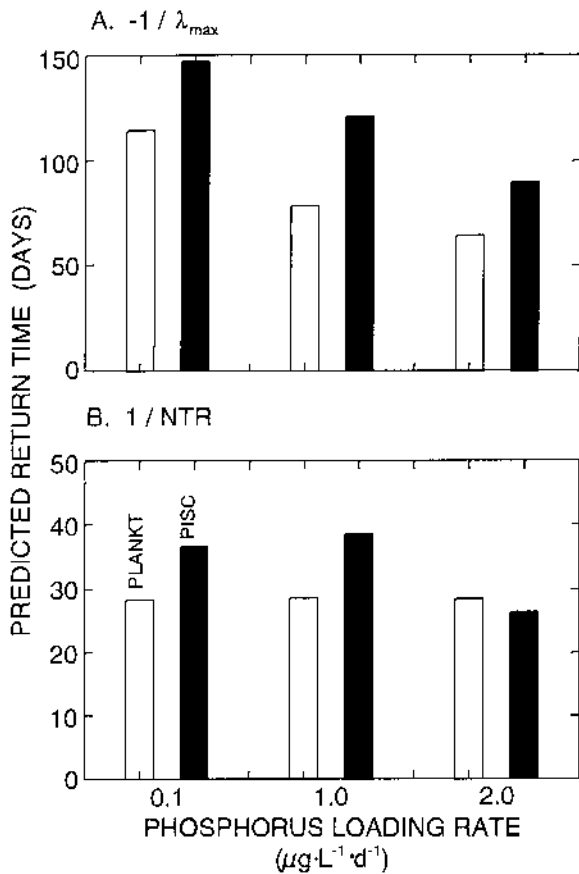


FIG. 2. Return times predicted by the resilience indices for planktivore- (open bars) and piscivore-dominated (filled bars) food webs at each baseline phosphorus loading rate. (A) $-1/\lambda_{max}$ (the dominant eigenvalue of the linearized system); (B) $1/NTR$ (the average nutrient turnover rate).

ranged in magnitude from 5 to 50 μg/L. Preliminary investigations indicated that all food web-baseline phosphorus loading combinations responded little to pulse perturbations of available phosphorus <5 μg/L and failed to recover from pulses >50 μg P/L.

There are many ways to measure resilience after a perturbation has occurred (e.g., Bloom 1980, DeAngelis 1980, 1992, Steinman et al. 1991, 1992). Resilience is most commonly defined in terms of the recovery of each system component to its predisturbance state (Pimm 1984). As a result, most measures require enormous amounts of data on the perturbation and pre-perturbation state of each component, information that may be difficult or impossible to obtain in the field. In a model, this is less difficult. We began by calculating the displacement between reference and perturbed simulations, summed over all trophic levels:

$$D_N(t) = \sqrt{\sum_{i=1}^n [N_{pi}(t) - N_{ri}(t)]^2 / [N_{ri}(t)]^2} \quad (3)$$

N_{pi} is the amount of nutrient stored in trophic level i

in the perturbed simulation, N_{ri} is the amount of nutrient stored in trophic level i in the reference simulation, n is the number of trophic levels, and t is the time since perturbation. $D_N(t)$ was determined for each day from the day of perturbation until the end of the simulation. Percent displacement was obtained by multiplying $D_N(t)$ by 100.

Return times were then calculated from formulas developed in other modeling studies. The first proposed formula for return time integrated the displacement [$D_N(t)$] over the period from the time of perturbation ($t = 0$) through the end of a simulation (T_F ; Harte and Morowitz 1975, O'Neill 1976):

$$\text{unscaled return time} = \int_{t=0}^{T_F} D_N(t) dt \quad (4)$$

Trapezoidal integration at 1-d intervals was used to approximate all integrals.

In more recent literature, return times have been calculated from the integral of displacements, scaled by the displacement on the day of the perturbation [$D_N(0)$; DeAngelis 1980, 1992, DeAngelis et al. 1989a]:

return time scaled by initial displacement

$$= \int_{t=0}^{T_F} \frac{D_N(t)}{D_N(0)} dt \quad (5)$$

However, when there are delays between the perturbation and the time of the maximum displacement, Eq. 3 could be misleading (DeAngelis et al. 1989a). Consequently we also tried a third measure, the integral of the displacements scaled by the maximum displacement observed after the perturbation [$D_N(m)$]:

return time scaled by maximum displacement

$$= \int_{t=0}^{T_F} \frac{D_N(t)}{D_N(m)} dt \quad (6)$$

Return times calculated from Eqs. 5 and 6 estimate the mean time it takes for the displacement of each trophic level to decay to e^{-1} (37%) of its initial or maximum value (DeAngelis 1992). As a result, return times could be quite long even for a tiny perturbation. We were interested in recovery rates following perturbations large enough to cause a change in the system, and so did not calculate scaled return times when initial or maximum displacements were <1.0 (100%).

RESULTS

Resilience indices

Return times estimated from the dominant eigenvalue (λ_{max}) supported the hypotheses that resilience decreases with increased food web length (Pimm and Lawton 1977) and increases with increased nutrient

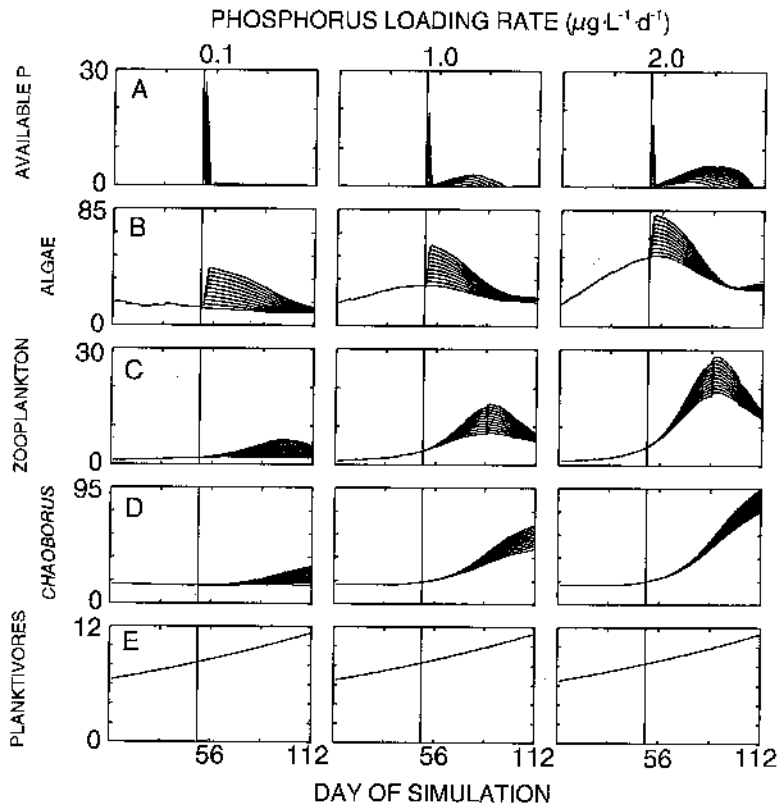


FIG. 3. Response of a planktivore-dominated food web to 1-d nutrient pulses at each baseline nutrient loading rate. In each panel, the vertical line indicates the day of perturbation and each curve shows the response following a different pulse; greater responses correspond to greater pulse magnitudes. Columns denote baseline phosphorus loading rate; rows indicate each of the trophic levels considered: (A) available phosphorus, (B) algae, (C) zooplankton, (D) *Chaoborus*, and (E) planktivorous fish. Units of all panels are phosphorus concentration, $\mu\text{g/L}$.

loading (DeAngelis et al. 1989a). That is, return times calculated from λ_{max} were greater when piscivores were dominant and when baseline phosphorus loading rates were lower (Fig. 2A).

In contrast, return times estimated from NTR did not support hypotheses for either food web structure or baseline phosphorus loading rate. NTR-derived return times were higher (resilience was lower) for the piscivore-dominated food web at 0.1 and 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, but not at 2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ phosphorus loading (Fig. 2B). In addition, return times did not decrease with baseline phosphorus loading rate (Fig. 2B).

Return times based on λ_{max} were predicted to differ by $\approx 30\text{--}40$ d for planktivore- and piscivore-dominated food webs (Fig. 2A). Food web differences were much smaller for NTR-derived return times, ≈ 10 d at 0.1 and 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ and ≈ 2 d at 2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ phosphorus loading (Fig. 2B).

All return times calculated from λ_{max} were longer than 9 wk (Fig. 2A), suggesting that neither food web would recover from a perturbation between day 50 and the end of a simulation. In contrast, all return times calculated from NTR were < 6 wk (Fig. 2B), suggesting that recovery from perturbation would occur before the end of the simulation.

Model response to pulse perturbations

Successive increases in the available phosphorus, algae, zooplankton, and *Chaoborus* compartments were observed as nutrient pulses were transmitted up each food web (Figs. 3 and 4). Nutrients did not reach the top predator, fishes, in either food web. Instead, they accumulated in *Chaoborus* (Figs. 3 and 4). In the planktivore-dominated food web, available phosphorus, algae, and zooplankton returned smoothly to reference levels before the end of the summer simulation at all three baseline phosphorus loading rates (Fig. 3). In the piscivore-dominated food web, recovery was more irregular. Available phosphorus accumulated following large pulses at each of the baseline phosphorus loading rates (Fig. 4A). At phosphorus loading of 0.1 and 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, postperturbation recovery of algae and zooplankton tended to overshoot reference levels, although both returned smoothly to reference levels at 2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ (Fig. 4B, C).

The displacement between reference and perturbed simulations increased with pulse size (Fig. 5). Displacements increased slightly between baseline phosphorus loading rates of 0.1 and 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, but decreased sharply between 1.0 and 2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ (Fig. 5). Initial

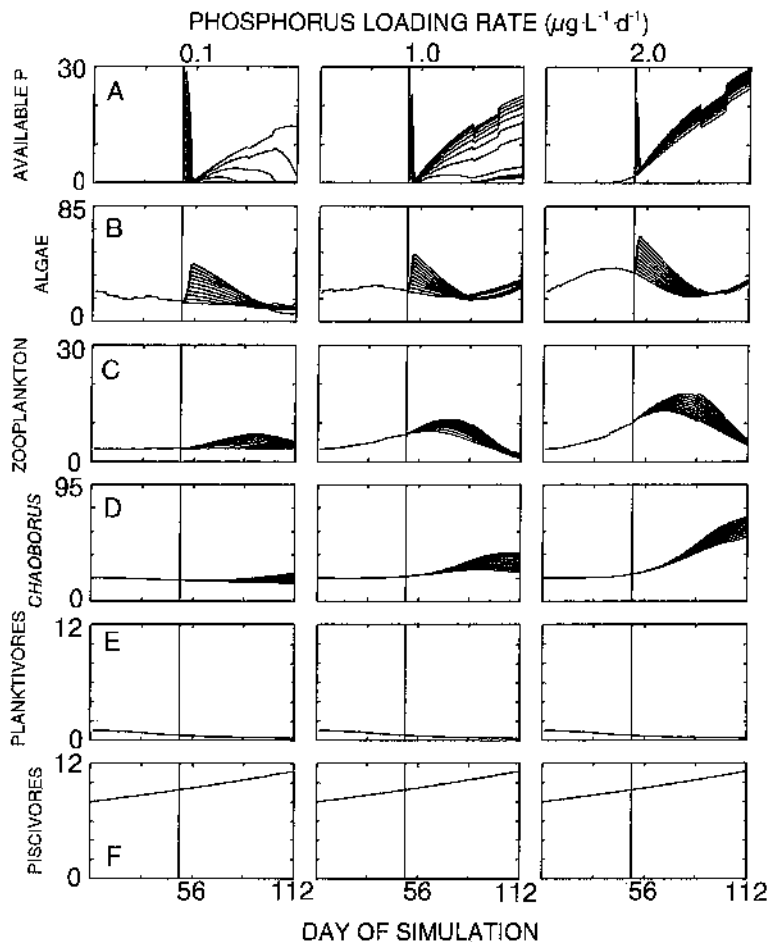


FIG. 4. As in Fig. 3, except the responses are for a piscivore-dominated food web. Row (F) is piscivorous fish.

and maximum displacements coincided for the piscivore-dominated food web, but not for the planktivore-dominated food web, particularly at $2.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ baseline phosphorus loading (Fig. 5). These measures indicated that the piscivore-dominated food web was displaced farther than the planktivore-dominated food web following phosphorus pulses $<10 \mu\text{g}/\text{L}$ at $0.1 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ and $<20 \mu\text{g}/\text{L}$ at $1.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$. However, the planktivore-dominated food web was displaced more than the piscivore-dominated food web when pulses were $>20 \mu\text{g}/\text{L}$ at all three baseline phosphorus loading rates (Fig. 5).

Measurements of resilience

Return times varied with measure, pulse size, food web structure, and baseline phosphorus loading rate (Fig. 6). Unscaled return times increased steadily with increasing pulse size (Fig. 6A), while return times scaled by the initial and maximum displacements changed less consistently with pulse size (Fig. 6B, C). Return times increased from 0.1 to $1.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ baseline phosphorus loading and decreased from 1.0 to $2.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$. Differences between food webs were ≈ 7

yr for the unscaled return time (Fig. 6A), and 10–20 d for initial and maximum displacement return times (Fig. 6B, C). At $0.1 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ baseline phosphorus loading, the piscivore-dominated food web recovered more quickly from small pulses while the planktivore-dominated food web recovered more quickly from larger pulses (Fig. 6). The threshold between “small” and “large” pulses was $35 \mu\text{g}/\text{L}$ for the unscaled return time (Fig. 6A) and $10 \mu\text{g}/\text{L}$ for initial or maximum return times (Fig. 6B, C). At $1.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ phosphorus loading, all three measures indicated that the planktivore-dominated food web had shorter return times regardless of pulse size (Fig. 6). At $2.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ phosphorus loading, return times in the piscivore-dominated food web were shorter than in the planktivore-dominated food web following nearly all pulses (Fig. 6).

Indices vs. measures

We compared the qualitative and quantitative consistency of the resilience indices (λ_{max} and NTR) with measured recovery rates (Table 2). Qualitatively, both λ_{max} and NTR predicted that the planktivore-dominated food web would be more resilient at 0.1 and 1.0

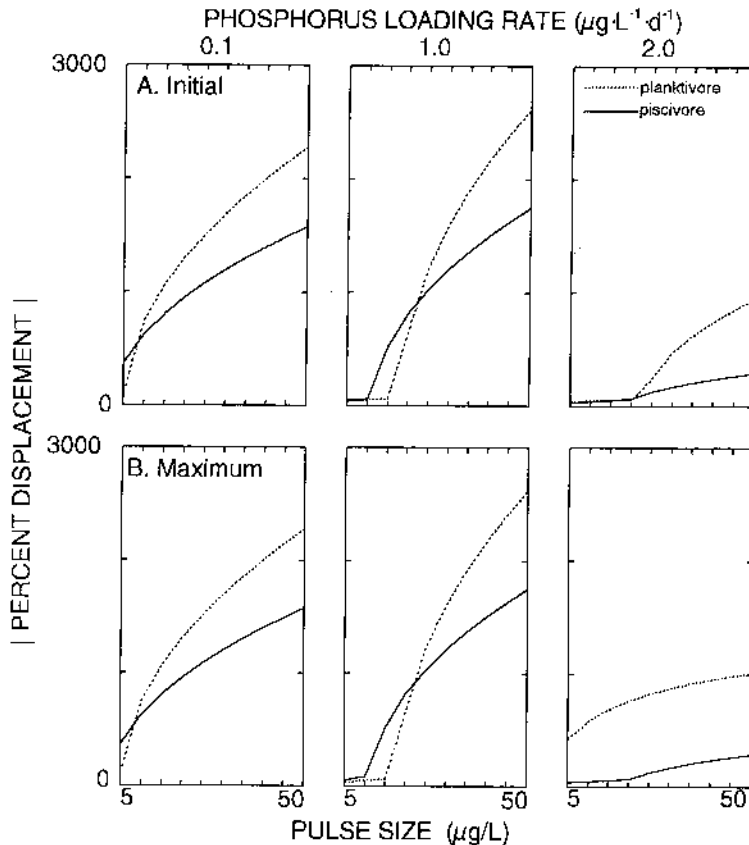


FIG. 5. Percent displacements calculated from simulations of planktivore- (thin dotted line) and piscivore-dominated (bold line) food webs following pulse perturbations. Percent displacement was calculated as the square root of the sum of squared differences between perturbed and reference simulations, divided by the reference simulation value, times 100. Columns indicate baseline phosphorus loading rate; rows indicate (A) initial (on day 50, the day of perturbation) and (B) maximum (highest observed from day 50 to 112) displacement.

$\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ baseline phosphorus loading (Table 2). Only NTR correctly predicted that the piscivore-dominated food web would be more resilient at $2.0\ \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ phosphorus loading (Table 2). Quantitatively, NTR indicated that recovery would take 30–50 d (Fig. 2), about the same amount of time as the resilience measures (Fig. 6), while λ_{max} indicated that recovery from perturbation would take longer than the period of simulation (≈ 100 –150 d).

DISCUSSION

Model response to pulse perturbations

Pulse perturbations of nutrients were passed rapidly from available phosphorus to algae, zooplankton, and *Chaoborus*, but not to the fishes (Figs. 3 and 4). The nutrient bottleneck could arise for a number of reasons, including slow fish growth rates and *Chaoborus* diel vertical migrations. It may be unrealistic to expect observable increases in fish growth due to one-time nutrient pulses, since fish growth can be minimal even with daily nutrient additions (Mazumder et al. 1992). Fish in Peter and Paul lakes are generally benthic feed-

ers whose diets are supplemented by feeding on zooplankton and *Chaoborus* when they are available (He et al. 1993). Vertical migration separates *Chaoborus* from fish, allowing coexistence in the field (Luecke 1986) and ensuring minimal (<10%) fish consumption of *Chaoborus* standing stock in this model.

The relatively smooth recovery of available phosphorus, algae, and zooplankton in the planktivore-dominated food web (Fig. 3) contrasted with the more irregular recovery of the piscivore-dominated food web (Fig. 4). In the piscivore-dominated food web, large zooplankton overgrazed the postperturbation algal bloom, causing algae and then zooplankton to decline below reference levels. Available phosphorus accumulated following large pulses. Zooplankton grazing tightly controlled algal response to nutrient additions in the piscivore-dominated simulations, with important implications for resilience.

Measurements of resilience

Return times calculated in different ways agreed qualitatively but not quantitatively for pulses $> 5\ \mu\text{g}/\text{L}$ (Fig. 6). Return times that were not scaled by displace-

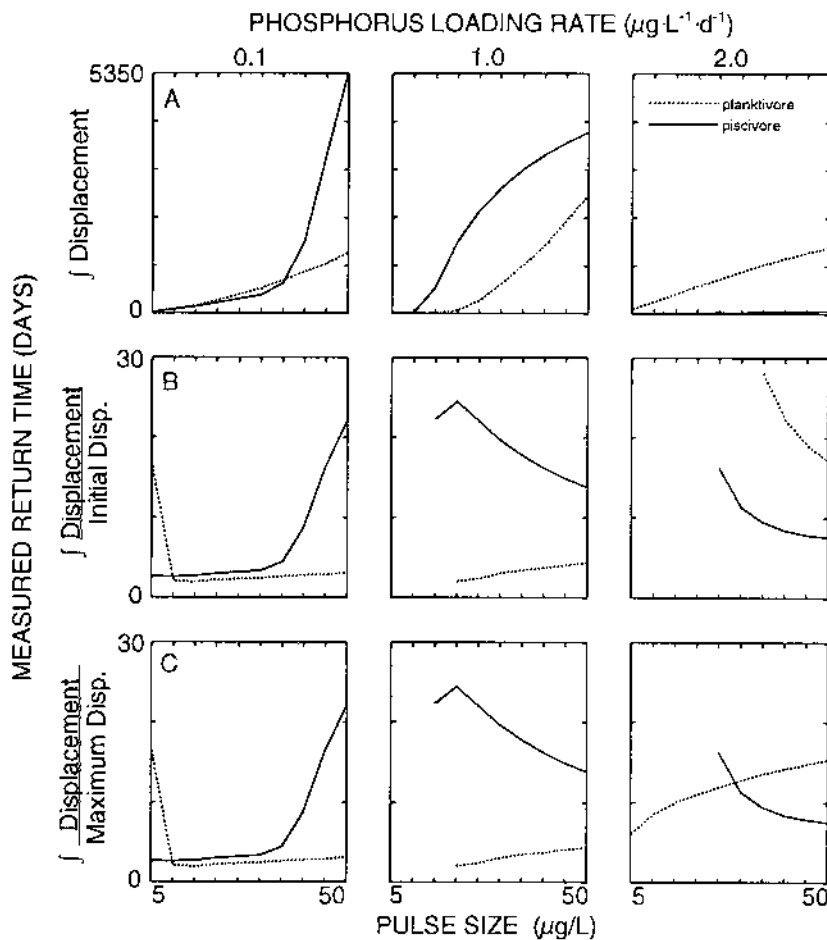


FIG. 6. Measured return times for perturbed planktivore- (thin dotted line) and piscivore-dominated (bold line) food webs. Columns indicate baseline phosphorus loading rate; rows indicate different ways of integrating the displacements to determine return time. (A) Integral of the displacement, (B) integral of the displacements divided by the initial displacement, and (C) integral of the displacement divided by the maximum displacement. Missing data from panels (B) and (C) indicate that the displacements were < 1.0 and therefore return times were not calculated.

ment size were remarkably long (many years), although scaled return times were < 1 mo. Most of the system recovered from the perturbation before the end of the simulation (Figs. 3 and 4), suggesting that the scaled return times are better measures of system behavior. Return times scaled by the initial and maximum displacement differed only when baseline phosphorus loading rates reached $2.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ in the planktivore-dominated food web (Fig. 6B, C). For this nutrient-food web combination, initial displacements vastly underestimated the delayed, maximum displacement (Fig. 5). Apparently maximum, and not initial, displacements are the appropriate reference level if return times are scaled by perturbation size.

Measured return times varied with pulse size (Fig. 6), suggesting that perturbation magnitude can affect conclusions about the relationships between resilience, food web structure, and baseline nutrient loading rate. Differences between resilience studies, therefore, may be due primarily to choice of perturbation, rather than inherent differences among systems. The effects of both

perturbation type and magnitude need to be explored more thoroughly for different types of ecosystems.

General statements about how resilience changes with food web structure or nutrient loading may not be possible for complex systems (DeAngelis et al. 1989a). The resilience of model food webs changed with pulse size and how resilience was measured and may change with perturbation type. Below, we focus on qualitative conclusions in the range of perturbations for which responses were relatively consistent.

Measured resilience, food web structure, and baseline nutrient loading rate

In our model, measured return times indicated that food web length and baseline phosphorus loading rate interacted to determine resilience. Resilience decreased with food web length at 0.1 and $1.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ baseline phosphorus loading, but not at $2.0 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ (Table 2). This switch appears to be related to altered nutrient cycling patterns.

TABLE 2. Qualitative effects of food web structure and baseline phosphorus loading rate on indices and measures of resilience. Resilience was estimated from λ_{max} , NTR, and the inverse of the return times shown in Fig. 6. Plk and pisc are abbreviations for planktivore- and piscivore-dominated food webs, respectively, and " $a > b$ " indicates that a is more resilient than b .

		Baseline phosphorus loading rate ($\mu\text{g P}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)		
		0.1	1.0	2.0
A) Indices	λ_{max}	plk > pisc	plk > pisc	plk > pisc
	NTR	plk > pisc	plk > pisc	pisc > plk
B) Measures	Unscaled	*	plk > pisc	pisc > plk
	Scaled by the initial displacement	plk > pisc†	plk > pisc	pisc > plk
	Scaled by the maximum displacement	plk > pisc†	plk > pisc	‡

* The effect of food web structure varied with pulse size. The piscivore-dominated food web was more resilient to pulses $\leq 35 \mu\text{g/L}$, but the planktivore-dominated food web was more resilient following pulses $> 35 \mu\text{g/L}$.

† For pulses $> 5 \mu\text{g/L}$.

‡ The planktivore-dominated food web was more resilient to pulses $\leq 25 \mu\text{g/L}$; the piscivore-dominated food web was more resilient to pulses $> 25 \mu\text{g/L}$.

The planktivore-dominated food web was more resilient than the piscivore-dominated food web at 0.1 and 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ baseline loading (Table 2). This result supports the hypothesis that resilience decreases with increased food web length (Pimm and Lawton 1977, Carpenter et al. 1992). Shorter food webs are thought to have greater nutrient processing rates, in part because there are fewer nutrient pathways (Pimm and Lawton 1977). In aquatic systems, nutrient dynamics may be faster in shorter food webs, since body size and generation time tend to be greater at higher trophic levels (Carpenter et al. 1992).

At high baseline phosphorus loading (2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$), the more complex, piscivore-dominated food web was more resilient. Because resilience is related to the efficiency with which food webs capture and process energy and nutrients (DeAngelis 1980), the higher resilience of the longer food web could result from more efficient nutrient processing (DeAngelis et al. 1978). In our model, nutrients enter the biota via algal uptake. The efficiency with which these nutrients are passed up the food web depends on the zooplankton community. Zooplankton in planktivore-dominated food webs tend to be smaller, less efficient grazers than zooplankton in piscivore-dominated food webs (McQueen et al. 1986). Consequently, nutrient flow from algae to zooplankton is slower in planktivore-dominated food webs than piscivore-dominated food webs, simply because of zooplankton community structure. At high loading, the greater transfer efficiency of nutrients within the piscivore-dominated food web may have offset the longer flow paths of the more complex food web.

In this model, quantitative differences in resilience due to food web structure and baseline phosphorus loading rate were quite small. Differences in return times scaled by the initial or maximum displacement were < 25 d and usually ≈ 10 d (Fig. 6B, C). In a different lake ecosystem model, the addition of piscivores led to whole-system return times (computed from our Eq. 5) that differed by < 10 d from piscivore-free simulations (DeAngelis et al. 1989a; Figs. 12 and 13). If

the differences in real ecosystems are as small as those observed in the model food webs, the effects of food web structure or baseline phosphorus loading rate on resilience may be difficult to detect in the field. Field estimates of NTR predict that return times will differ by < 1 mo, while λ_{max} predicts greater differences. For example, average phosphorus turnover rates determined in a real lake (Carpenter et al. 1992) indicate that the return times of contrasting food webs at low baseline loading rates would differ by ≈ 12 d. Carbon turnover rates of four different lakes (Richey et al. 1978) indicated that return times would differ by ≈ 30 d. However, measurements of λ_{max} suggest that return times of contrasting food webs may differ by 180 d (Carpenter et al. 1992). More field studies are needed to determine the extent to which estimated and measured return times vary among lakes.

A carefully planned ecosystem experiment could answer several of the questions raised by this modeling study. For example, where do nutrients accumulate following pulse perturbations? Which resilience measures and indices work best? Are food web differences in resilience measurable? Do our conclusions about the relationships between resilience and food web structure hold for real ecosystems? One way to test these ideas would be to contrast the recovery of lakes with different food webs from one-time pulse perturbations. In the model, a single pulse perturbation seems to disappear from lower trophic levels within 9 wk (Figs. 3 and 4), suggesting that there should be few residual effects of such a perturbation. Pulses $> 5 \mu\text{g/L}$ are most likely to give an unequivocal result about food web effects, especially at baseline phosphorus loading rates up to 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ (Fig. 6). Difficulties in planning such experiments include defining the reference state, finding a time scale suitable for monitoring recovery, and finding lakes with suitable food webs and baseline phosphorus loading rates. One possibility may be to take advantage of a natural experiment, for example, a single high rainfall event that creates loading pulses large enough to track through the rest of the ecosystem.

λ_{max} and NTR as predictive indices of
resilience

Predictions about resilience based on the indices generally corresponded to direct measurements of resilience (Table 2). Both λ_{max} and NTR were correct in predicting that the planktivore-dominated food web would be more resilient at 0.1 and 1.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ baseline phosphorus loading, but only NTR predicted that the piscivore-dominated food web would be more resilient at 2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ (Table 2). In addition, the quantitative agreement of NTR and the measured recovery rates was much greater than the agreement between λ_{max} and the measures (Figs. 2 and 6).

These results suggest that nutrient turnover rate was a sufficient predictor of recovery from pulse perturbations of nutrient inputs, at least for simulated lakes with extreme food web configurations and baseline phosphorus loading rates up to 2.0 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$. The utility of NTR is corroborated by the importance of water residence times (an important component of NTR) in empirical eutrophication models (Vollenweider 1968, Schindler 1978). NTR is easy to measure with relatively few arbitrary conditions, quite unlike our direct measurements of resilience, which depended on arbitrary choices of which system components to monitor, the perturbation size, and the preperturbation state. These choices complicate the cross-system comparisons and predictions needed to make ecological assessment, impact, and restoration studies. To guarantee comparable results across systems or experimental setups, such arbitrary conditions must be standardized. This standardization will be difficult for ecosystem perturbations. However, if nutrient turnover rate proves to be a suitable index of resilience in a variety of systems, these standardizations may not be necessary. Comparisons of NTR and measurements of resilience in real ecosystems may validate this approach.

Despite the challenges of measurement, ecosystem resilience remains a central concept that underlies powerful theoretical results (Pimm 1984, 1991, DeAngelis 1992), has important implications for ecosystem management (National Research Council 1992), and continues to attract the interest of ecologists studying a wide variety of systems (DeAngelis et al. 1989b). The advancement of measurable, predictive indices of ecosystem resilience would open a significant body of ideas to testing, elaboration, and application.

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