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RESILIENCE AND RESISTANCE OF A LAKE PHOSPHORUS CYCLE BEFORE AND AFTER FOOD WEB MANIPULATION

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Abstract.—Parameters of a phosphorus cycling model were estimated for two configurations of a lake ecosystem. The piscivore-dominated configuration had one more trophic level than the planktivore-dominated configuration. We derived four main conclusions from analysis of the model. (1) Results support the argument of DeAngelis et al. that turnover rate of a limiting nutrient is directly related to ecosystem resilience. (2) Results support the hypothesis of Pimm and Lawton that longer food chains are less resilient. (3) Inputs of phosphorus to the pelagic system derived from inshore feeding by fishes were a large flux, which is comparable to inputs from physical-chemical fluxes. (4) Algal (seston) standing crops, unlike all other compartments, were less sensitive to phosphorus inputs in the piscivore-dominated system. Consistent with the trophic cascade hypothesis, the piscivore-dominated system had higher herbivore standing crops and lower algal standing crops than the planktivore-dominated system. Changes in trophic structure that derive from trophic cascades can be viewed as changes in the phosphorus cycle driven by fishes.

Ecologists have developed a rich theory centered on stability, resilience, and resistance of communities and ecosystems. Stability, resilience, and resistance are fundamental to questions about length of food chains and complexity of food webs (Pimm 1984) and responses of nutrient and contaminant cycles to perturbation (Webster and Patten 1979; DeAngelis et al. 1989*a*, 1989*b*). These concepts offer the hope of quantitative assessment and prediction in applied ecology, in which many questions involve the dynamics of systems after perturbation. Definitions of resilience, resistance, and several types of stability are found in many sources (Holling 1973; Pimm 1984; DeAngelis et al. 1989*a*). Our article addresses resilience, the rate at which a system returns to equilibrium after disturbance, and resistance, the inverse of the sensitivity of a system to a change in inputs.

While theoretical studies of resilience and resistance provide many crisp, readily interpreted results, empirical studies are fewer and more ambiguous (DeAngelis et al. 1989*a*). Few experimentalists have undertaken the calculations necessary to test ideas about resilience and resistance (Pimm 1984). Few studies

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provide data from enough components of an ecosystem to estimate resistance and resilience. Intersystem comparisons are often difficult to make because of different physical-chemical conditions and different methods for estimating nutrient fluxes. Studies that can overcome these problems are needed to test several prominent ideas about resilience and resistance in ecosystems (Pimm 1984; DeAngelis et al. 1989*a*).

We have the opportunity to compare resilience and resistance for the phosphorus cycle of a lake ecosystem before and after food web manipulation (see below). Abiotic phosphorus inputs were similar before and after manipulation. Therefore, resilience and resistance of two contrasting ecosystem configurations could be compared under similar physical-chemical conditions. This comparison enabled us to test the hypotheses that ecosystems with longer food chains are less resilient (Pimm and Lawton 1977), turnover rate of a limiting nutrient increases as ecosystem resilience increases (DeAngelis et al. 1989*a*, 1989*b*), and primary producers are more resistant to changes in nutrient input in ecosystems with four trophic levels than in ecosystems with three trophic levels (Carpenter and Kitchell 1988).

ECOSYSTEM EXPERIMENT

Tuesday Lake, a small (1.2 ha) steep-sided (maximum depth = 18.5 m) bog lake near Land o' Lakes, Wisconsin (89°32′W, 46°13′N), was studied before and after a food web manipulation in 1985 (Carpenter et al. 1987; Carpenter and Kitchell, in press). Data that allowed us to estimate parameters of the phosphorus flow model (fig. 1) were collected during the summer-stratified seasons of 1984–1986. The influences of temporal and spatial scales on phosphorus flux estimates are unavoidable. We used the period of summer stratification as a natural time scale that is important in the metabolism of lakes (Carpenter et al. 1991). Because the lake is steep sided, littoral zone development is minimal. Therefore, our sampling effort, and this analysis, focused on the pelagic food web. However, flows of phosphorus from the littoral zone into the pelagic food web were estimated (see below).

In 1984, planktivorous minnows were at the top of the food web, and the ecosystem had five state variables (all except the piscivorous fishes; fig. 1). Premanipulation plankton communities were described by Carpenter et al. (1987). During 1985, 56.4 kg of minnows were removed by trapping and were replaced by 57.6 kg of piscivorous largemouth bass (Carpenter et al. 1987). This near-equivalent exchange of fish biomass reconfigured the food web without appreciably changing the standing stock of phosphorus. After manipulation, the ecosystem had six state variables (fig. 1). Postmanipulation plankton communities were described by Carpenter et al. (1987) and Elser and Carpenter (1988). The year 1985 was one of highly variable transitional dynamics, and the seasonal means needed to estimate the parameters of the model have little meaning during this time. Also, resilience and resistance are not defined for nonequilibrial dynamics (Pimm 1984; DeAngelis et al. 1989*a*). In contrast, 1984 and 1986 were years of more modest fluctuations that could be reasonably characterized by seasonal averages. This article compares models for Tuesday Lake under the three-trophic-level configuration of 1984 and the four-trophic-level configuration of 1986.

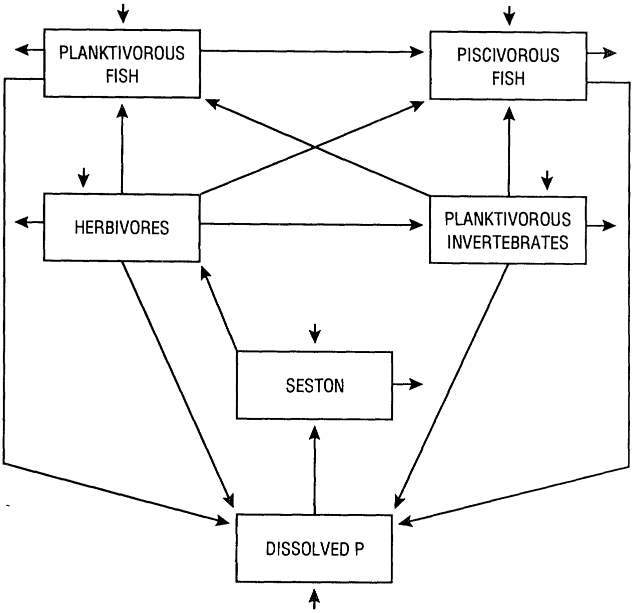

FIG. 1.—Diagram of the phosphorus compartments and flows analyzed in this study. In Tuesday Lake, seston consisted mainly of phytoplankton. The herbivores were zooplankton, including crustaceans and rotifers. The invertebrate predator was the phantom midge, *Chaoborus punctipennis*. Planktivorous fishes were minnows in 1984 and young-of-the-year bass in 1986. Piscivorous fishes were not present in 1984 and were juvenile and adult bass in 1986.

MODEL

The phosphorus cycling model represents the photic zone of a lake during summer (fig. 1). Six compartments are represented: dissolved phosphorus available for uptake (soluble reactive phosphorus [SRP]), seston (mainly phytoplankton but also including bacteria, protozoans, and detritus), herbivorous zooplankton, the invertebrate planktivore *Chaoborus,* planktivorous fishes, and piscivorous fishes. The model is a compromise between the need to provide adequate biological detail and the pragmatisms of estimating the coefficients. We included the major components of the Tuesday Lake ecosystem as represented in earlier modeling and data articles (Carpenter and Kitchell 1987; Carpenter et al. 1987).

For resilience and resistance calculations, we analyzed the model using the linear nutrient cycling framework of Harrison and Fekete (1980) and DeAngelis et al. (1989*a*, 1989*b*):

$$d\mathbf{x}/dt = \mathbf{A}x + \mathbf{z}, \tag{1}$$

where $\mathbf{x}$ is the vector of nutrients in each compartment, $\mathbf{z}$ is the vector of inflow rates from outside the system, and $\mathbf{A}$ is the flow-rate matrix for transfers between compartments and transfers out of the system. The diagonal entries of $\mathbf{A}$, a_{jj}, are the proportions of the nutrients in compartment j that flow out of compartment j

in each time step. That is, $-a_{jj}x_j$ is the outflow rate from compartment j, and $1/a_{jj}$ is the turnover time of compartment j. The off-diagonal entries of **A**, a_{ij}, are the proportions of nutrients in compartment j that flow to compartment i in each time step, so $a_{ij}x_j$ is the flow rate from compartment j to compartment i. It is useful to define a_0 as a vector of outputs separate from **A**, so, by conservation of mass,

$$a_{jj}x_j = -a_{0j}x_j - \sum_i a_{ij}x_j . \tag{2}$$

The vector of equilibrium nutrient levels is

$$\mathbf{x}^* = -\mathbf{A}^{-1}\mathbf{z}. \tag{3}$$

Resilience is the rate at which the system approaches equilibrium (Harrison and Fekete 1980). If all the eigenvalues of **A** are negative, then the model is stable and resilience is proportional to $\lambda_{\max}$, the eigenvalue closest to zero. After perturbation, a system with high resilience returns quickly to equilibrium; a system with low resilience returns slowly to equilibrium. In the model, since resilience depends only on the elements of **A**, it is independent of changes in nutrient inputs, **z**.

The sensitivity of resilience to changes in the flow matrix was calculated from the formula of Caswell (1978):

$$d\lambda_{\max}/da_{ij} = \mathbf{w}_i\mathbf{v}_j , \tag{4}$$

where **w** is the left eigenvector of **A** and **v** is the right eigenvector of **A**. In the case of the output vector,

$$d\lambda_{\max}/da_{0j} = -\mathbf{w}_i\mathbf{v}_j \tag{5}$$

by applying the chain rule and equation (4) to the differential of equation (2).

Resistance is inversely related to the magnitude of displacement from equilibrium following a perturbation (Harrison and Fekete 1980). Suppose Δz_i is a perturbation to a nutrient input, Δa_{ij} is a perturbation to an element of the flow matrix, and $\mathbf{\Delta A}$ is a matrix of zeros except for perturbation(s) Δa_{ij}. Then we calculate a perturbation vector

$$p_i = \Delta z_i + \sum_j \Delta a_{ij}x_j^* . \tag{6}$$

The vector of displacements from equilibrium, $\mathbf{\Delta x}^*$, is

$$\mathbf{\Delta x}^* = -(\mathbf{A} + \mathbf{\Delta A})^{-1}\mathbf{p} . \tag{7}$$

Resistance can be calculated for any perturbation. A system that has small values of $\mathbf{\Delta x}^*$ does not change much following perturbation and is therefore deemed resistant; a system that has large values of $\mathbf{\Delta x}^*$ changes a lot after perturbation and is therefore not resistant.

The sensitivity, or inverse resistance, of the ecosystem to a change in nutrient input is an important issue in many aquatic systems. We calculated the sensitivity

TABLE 1

Phosphorus Flow Matrices for Tuesday Lake in 1984 and 1986

Compartment	SRP	Seston	Zooplankton	*Chaoborus*	Planktivore	Piscivore
1984:						
SRP	−.9503	0	.013	.0056	.0257	. . .
Seston	.95	−.059	0	0	0	. . .
Zooplankton	0	.029	−.2622	0	0	. . .
Chaoborus	0	0	.2	−.1752	0	. . .
Planktivore	0	0	.0192	.0026	−.0389	. . .
1986:						
SRP	−.9503	0	.069	.0002	.0027	.0034
Seston	.95	−.18	0	0	0	0
Zooplankton	0	.15	−.2569	0	0	0
Chaoborus	0	0	.1	−.0138	0	0
Planktivore	0	0	.0019	.0002	−.0124	0
Piscivore	0	0	0	.0001	.0028	−.0049

Note.—Units of all entries are d^{-1}; SRP is soluble reactive phosphorus. Columns are flow rates from the indicated compartment; rows are flow rates to the indicated compartment. Diagonal entries were calculated using eq. (2).

of the equilibrium compartment sizes to changes in the elements of the input vector:

$$dx_i^*/dz_j = s_{ij}. \tag{8}$$

Here s_{ij} is the appropriate element of $-\mathbf{A}^{-1}$. Equation (8) follows directly from equation (3).

FLUX ESTIMATES

Phosphorus fluxes were estimated from previously published information from Tuesday Lake for the June–August periods of 1984 and 1986 (table 1). Estimating these fluxes required synthesis of a large body of previously published information. This synthesis is summarized in the next three subsections. For both limnological fluxes and fluxes to and from fish compartments, sources of data and assumptions are described. The third subsection gives the details of the flux calculations.

Limnological Data and Assumptions

Dissolved phosphorus represents P available for uptake by the biota. Methods for phosphorus and sedimentation rate measurements were described by Carpenter et al. (1986) and J. J. Elser et al. (1988). Phosphorus concentrations were reported by Carpenter et al. (1991). Phosphorus sedimentation rates from the photic zone, which have not previously been published, were 0.109 and 0.097 μg L^{-1} d^{-1} in 1984 and 1986, respectively.

The seston compartment consists mainly of algae but also includes suspended detritus, bacteria, and protozoans. We assumed that this consortium was capable of removing 95% of the dissolved phosphorus from the water each day. Inputs via algal colonization from sediments were assumed to be 0.1% of the maximum standing crop (Reynolds 1984). A sinking loss rate of 0.03 d^{-1} was calculated from the phytoplankton size distribution with equations from Reynolds (1984). Since diatoms are a negligible component of the summer phytoplankton (Carpenter et al. 1987; Elser and Carpenter 1988), our calculation was based on densities for nondiatom algae (Reynolds 1984). This loss rate is consistent with measured sedimentation rates (Carpenter et al. 1986).

Zooplankton analysis methods were detailed by Carpenter et al. (1987). Zooplankton phosphorus content was assumed to be 1.8% of dry mass (Peters and Rigler 1973). Inputs as eggs were assumed to be 0.1% of the maximum standing crop. Grazing rates were taken from Carpenter et al. (1988) for 1984 and Leavitt and Carpenter (1990) for 1986. Excretion of SRP was assumed to be 40% of ingestion (Peters and Rigler 1973). Losses by egestion were assumed to be 40% of ingestion (Grodzinski et al. 1975), and losses of exuviae were assumed to be 0.017 d^{-1} (Hallam et al. 1990).

Chaoborus analysis methods were detailed by M. M. Elser et al. (1987). Predation rates were estimated from M. M. Elser et al. (1987) and Carpenter and Kitchell (in press). Inputs from diapausing eggs were assumed to be 0.1% of maximum standing crop. Excretion was assumed to be 1% of consumption (Swift 1976). Egestion was assumed to be 29% of consumption (Cressa and Lewis 1986). Losses due to emergence and exuviae were estimated from instar-specific time course data (M. M. Elser et al. 1987; Carpenter and Kitchell, in press).

Fish Compartments: Data and Assumptions

Fish phosphorus excretion was estimated according to the mass balance equation $U = C - G - F$, where U is phosphorus excreted (urinary), C is phosphorus consumed, G is phosphorus allocated to growth, and F is fecal phosphorus loss. Seasonal estimates for C, F, G, and U were made over a 90-d period from late May to late August for dace in 1984 and young-of-the-year (YOY) bass, juvenile bass (<195 mm: fish ages 1 to <3 yr), and adult bass (>195 mm: fish ages 3 to >8 yr) in 1986. Dace and YOY bass were considered to be planktivores, and they consumed zooplankton, *Chaoborus,* and littoral foods in the model. Juvenile and adult bass were considered to be piscivores, and they consumed invertebrates (including zooplankton, *Chaoborus,* and littoral prey) as well as small fishes in the model. Fecal phosphorus loss was estimated with a phosphorus assimilation efficiency of 72%, based on laboratory estimates for yellow perch (Nakashima and Leggett 1980). Phosphorus allocated to growth was estimated by assuming that phosphorus sequestered by fish production was 0.5% of fish wet weight (Davis and Boyd 1978). Phosphorus consumed was calculated from estimates of prey consumption and prey phosphorus content. Prey consumption for largemouth bass (*Micropterus salmoides*) was estimated with a bioenergetics model developed by Rice et al. (1983). Prey consumption for northern redbelly dace (*Phoxinus eos*) was estimated with a similar bioenergetics model, for which parameters were presented by He (1986). Implementing these bioenergetics models required the growth and temperature history for an average individual, as well as information about the caloric content of both predators and prey.

He (1986) measured growth rates (g wet weight d^{-1}) for 0+ to 3+ dace. Growth rates for juvenile and adult bass were determined from field measurements; growth rates for YOY bass were estimated from Hamilton and Powles (1979). Bass and dace temperatures were assumed equal to water temperature, measured weekly at 1 m depth. Phosphorus was assumed to be 0.1% of wet weight for all nonfish prey and 0.5% of wet weight for fish prey (Nakashima and Leggett 1980). Energy content of fishes and their prey were assumed seasonally constant at values from the literature (Cummins and Wuycheck 1971; Rice et al. 1983; He 1986).

Dace population estimates for four age classes were given by He (1986). Adult bass population size was estimated by the Petersen capture-recapture method in May and August 1986 (Carpenter and Kitchell, in press). Bioenergetics model estimates showed that consumption by adult bass was relatively constant between age classes. Therefore, we divided the May adult bass population evenly among age classes and assumed 8% summer mortality. Young-of-the-year and juvenile bass populations were measured by Carpenter and Kitchell (in press).

Dace diets reported by He (1986) included periphyton, zooplankton, *Chaoborus,* and littoral benthic insects. Adult bass diets were analyzed from stomach contents in 1986 and included zooplankton, *Chaoborus,* littoral benthic insects, YOY bass, and juvenile bass (Carpenter and Kitchell, in press). Since only two juvenile bass stomachs were examined, juvenile bass diets were derived from adult bass diets. This was done by apportioning zooplankton and *Chaoborus* equally to the proportion of adult diets that consisted of juvenile bass, which resulted in juvenile bass diets similar to other studies (Clady 1974; Keast 1985; Hodgson and Kitchell 1987). No field diet information for YOY bass was available. Young-of-the-year bass diets were divided evenly between benthos and zooplankton in May (Keast and Eadie 1985), with increasing proportions of *Chaoborus* as the summer progressed.

Flux Calculations

All flux calculations were based on mean values over the summer-stratified seasons.

Excretion by zooplankton (a_{13}) or *Chaoborus* (a_{14}) was calculated as fC/S, where f is the fraction of ingested P that is excreted, C is consumption rate (mg P m^{-2} d^{-1}), and S is standing crop of the donor compartment (mg P m^{-2}). Excretion by fishes (a_{15} and a_{16}) was calculated as U/S, where U is excretion rate (mg P m^{-2} d^{-1}) and S is standing crop of the donor compartment (mg P m^{-2}).

Uptake of phosphorus by seston (a_{21}) and transfers of phosphorus by predation (a_{32}, a_{43}, a_{53}, a_{54}, a_{63}, a_{64}, and a_{65}) were calculated as C/S, where C is the consumption rate by the recipient compartment (mg P m^{-2} d^{-1}) and S is standing crop of the donor compartment (mg P m^{-2}).

Outputs from all compartments (a_{0j}) were calculated as output rate from compartment j (mg P m^{-2} d^{-1}) divided by standing crop of compartment j (mg P m^{-2}). Dissolved P output rate was based on the lake's hydraulic residence time. Seston output rate was equal to the phosphorus sedimentation rate. Output from the herbivorous zooplankton compartment included egestion and exuviae. Output from the *Chaoborus* compartment included egestion, exuviae, and emergence. For both herbivorous zooplankton and *Chaoborus,* egestion was calculated as fC/S, where f is the fraction of ingested P that is egested, C is consumption rate (mg P m^{-2} d^{-1}), and S is standing crop of the donor compartment (mg P m^{-2}). Outputs from the fish compartments included egestion and mortality. Diagonal elements of the flow matrix (a_{jj}) were calculated from the outputs and the off-diagonal elements of the flow matrix with equation (2).

Abiotic inputs of phosphorus were estimated from the mass balance equation $I = (\Delta c + s)/\Delta t$, where I is the net input of phosphorus, Δc is the change in photic zone concentration of total phosphorus over time interval Δt, and s is sedimentation over the time interval. This approach to estimating P inputs is appropriate in small lakes like Tuesday Lake, where airborne inputs from the surrounding terrestrial ecosystem can be large but highly variable in space and time (Cole et al. 1990).

Inputs of phosphorus to the seston compartment represent abiotic inputs of particulate P and colonization of the water column by benthic algae. Inputs to the zooplankton compartment represent hatching of resting eggs. Inputs to the *Chaoborus* compartment represent oviposition. Inputs of phosphorus to the fish compartments represent consumption of littoral foods. Consumption rate of littoral food items (mg P m^{-2} d^{-1}) was converted to concentration in the epilimnion by dividing by the mean depth of the epilimnion.

RESULTS

Littoral feeding by fishes was a major input of phosphorus to the pelagic system in both configurations of the food web (fig. 2). This flux exceeded the sum of the other phosphorous sources to the pelagic zone of Tuesday Lake.

The significance of phosphorus flux through fishes is illustrated by a comparison of dissolved phosphorus recycling from zooplankton, *Chaoborus,* and fishes (table 2). Zooplankton excretion is known to be a major source of nutrients for phytoplankton (Lehman 1980; J. J. Elser et al. 1988). Our data show that the summer average excretion of phosphorus by fishes is comparable to excretion by zooplankton. Under equilibrium conditions, excretion by fishes exceeds excretion by zooplankton.

All eigenvalues of both models were negative. Since the models were stable, calculations of equilibrium pool sizes, resilience, and resistance were made.

Summer average phosphorus pool sizes exceeded equilibrium values for all compartments in 1984 (fig. 3). Nonequilibrial pool sizes were sustained by high inputs of phosphorus via fishes feeding in the littoral zone. In 1986, summer average and equilibrium pool sizes were similar for dissolved phosphorus, seston, zooplankton, and planktivorous invertebrates. Summer average pool sizes in fishes were less than equilibrium values. The stocked fish populations would have to grow substantially to attain equilibrium levels.

The short food-chain configuration of 1984 was more resilient by all measures than the long food-chain configuration of 1986 (table 3). The equilibrium turnover rate, resilience, and return time differ by more than an order of magnitude be-

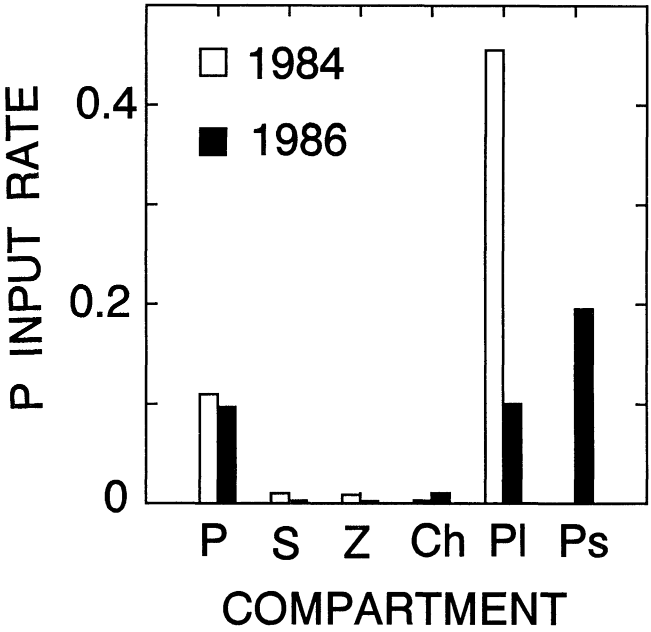

FIG. 2.—Phosphorus input rate (μg L^{-1} d^{-1}) to Tuesday Lake during June–August of 1984 and 1986 from sources described in the text. Compartments: *P*, dissolved P; *S*, seston; *Z*, zooplankton; *Ch*, *Chaoborus*; *Pl*, planktivorous fish; *Ps*, piscivorous fish.

TABLE 2

RATES OF PHOSPHORUS RECYCLING

Conditions	Zooplankton	*Chaoborus*	Fishes
Equilibrium:			
1984	.0114	.0057	.314
1986	.081	.0018	.174
Summer average:			
1984	.11	.017	.339
1986	.16	.0020	.047

NOTE.—Rates in μg L^{-1} d^{-1} from zooplankton, *Chaoborus*, and fish compartments are presented for equilibrium and summer average conditions in 1984 and 1986.

tween the two food web configurations. The summer average phosphorus turnover rate suggests that the shorter food chain was more resilient, but the difference between 1984 and 1986 is probably not significant. The growing, nonequilibrial fish population of 1986 caused summer average phosphorus turnover rate to be higher than the equilibrium turnover rate.

The sensitivity of resilience to elements of the flow matrix (table 4) can be regarded as an index of which flows control resilience or of the effect on resilience

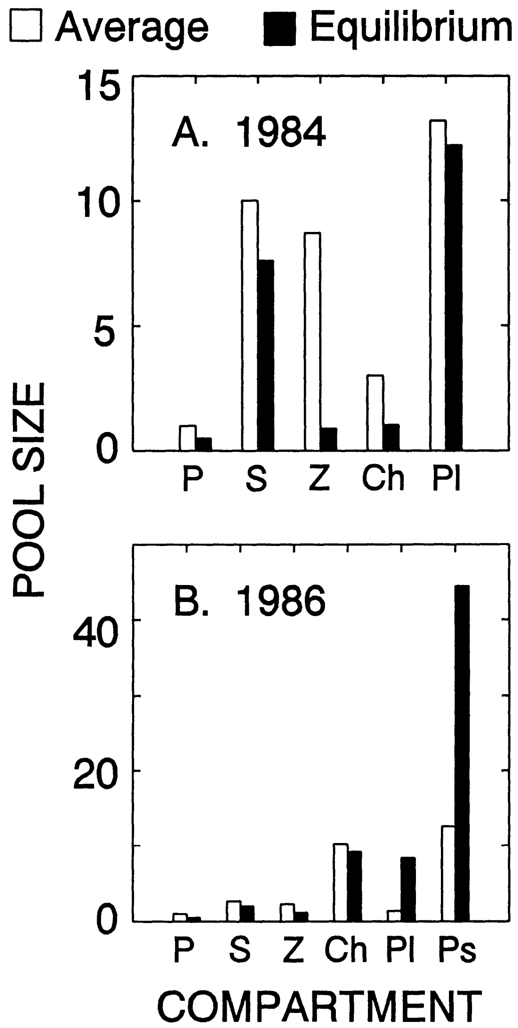

FIG. 3.—Equilibrium and summer average phosphorus pool sizes (μg L^{-1}) in Tuesday Lake for summers of (*A*) 1984 and (*B*) 1986. Compartments: *P*, dissolved P; *S*, seston; *Z*, zooplankton; *Ch*, *Chaoborus*; *Pl*, planktivorous fish; *Ps*, piscivorous fish.

of measurement errors in the flows. In 1984, resilience was relatively sensitive to grazing of seston by zooplankton, predation on zooplankton and *Chaoborus* by fishes, and phosphorus excretion by fishes. Resilience was also sensitive to losses of phosphorus by sedimentation of seston and death of planktivores (diagonal elements for seston and planktivores, respectively). In 1986, resilience was relatively sensitive to predation on *Chaoborus* by fishes and to outputs of phosphorus by death of piscivores.

The sensitivity of pool sizes to changes in phosphorus inputs (inverse resistance) was greatest in 1986 for all pools except seston, which was most sensitive

TABLE 3

Rates Derived from Phosphorus Flow Matrices

Property	1984	1986
P turnover rate at equilibrium	.0264	.00621
P turnover rate, summer average	.0168	.0140
Resilience	.0351	.00489
Return time	28.4	204.5

Note.—Phosphorus turnover rate (d^{-1}), resilience or system return rate (d^{-1}), and inverse resilience or return time (d) are presented for equilibrium and summer average conditions.

TABLE 4

Sensitivities of Resilience to Elements of the Flow Matrices

Compartment	SRP	Seston	Zooplankton	*Chaoborus*	Planktivore	Piscivore
1984:						
SRP	.0053	. . .	.0311	.0482	.1629	. . .
Seston	.0051	.2277	. . .	. . .	. . .	. . .
Zooplankton	. . .	.1326	.0173	. . .	.0906	. . .
Chaoborus	. . .	. . .	.0040	.0062	. . .	. . .
Planktivore	. . .	. . .	.1421	.2200	.7435	. . .
1986:						
SRP	.0001	. . .	.0003	.0040	.0005	.0204
Seston	.0001	.0005	. . .	. . .	. . .	. . .
Zooplankton	. . .	.0006	.0004	. . .	. . .	. . .
Chaoborus	. . .	. . .	.0006	.0071	. . .	. . .
Planktivore	. . .	. . .	.0062	.0773	.0097	. . .
Piscivore	. . .	. . .	. . .	.1941	.0244	.9822

Note.—Values of $d\lambda/da_{ij}$ (unitless) are presented. Diagonal elements are sensitivities to outputs. Columns are sensitivities to flows from the indicated compartment; rows are sensitivities to flows to the indicated compartment.

to changes in phosphorus inputs in 1984 (fig. 4). Dissolved phosphorus was more sensitive to changes in inputs in 1986 than in 1984 (fig. 4*A*). Changes in the external input of dissolved phosphorus and in littoral feeding by fishes had the greatest impact on dissolved phosphorus pool sizes. The seston phosphorus pool was more sensitive to changes in inputs in 1984 than in 1986 (fig. 4*B*). Inputs of dissolved phosphorus, seston phosphorus, and littoral feeding by fishes had the greatest effect on seston phosphorus pool sizes. Zooplankton phosphorus was more sensitive to changes in inputs in 1986 than in 1984 (fig. 4*C*). Zooplankton phosphorus responded to changes in all inputs except that of *Chaoborus*. The *Chaoborus* phosphorus pool was relatively insensitive in 1984 because minnows consumed few chaoborids (fig. 4*D*). In 1986, however, *Chaoborus* was sensitive to all inputs, especially those below it in the food web. The fish phosphorus pool was most sensitive to inputs by feeding in the littoral zone (figs. 4*D* and 4*E*). The planktivore pool was more sensitive to littoral zone feeding in 1986 than in 1984.

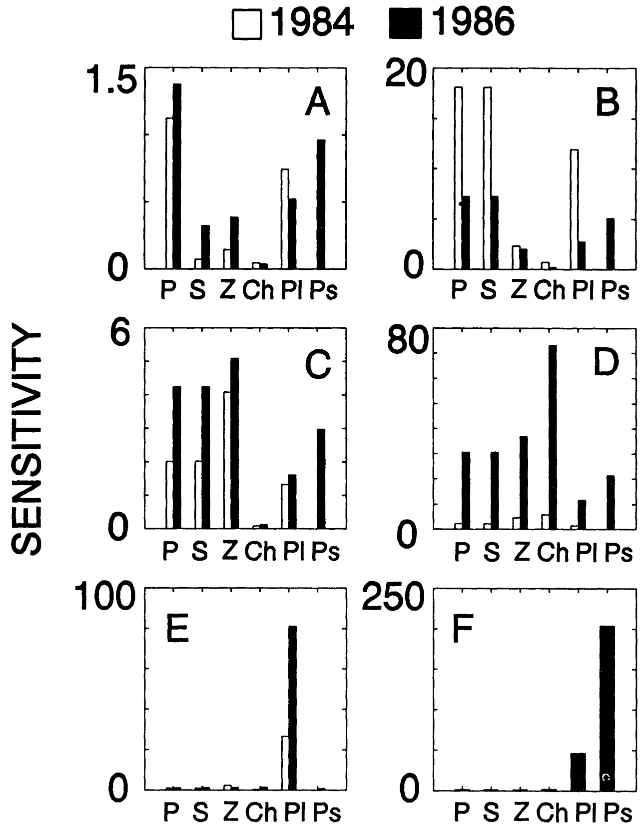

FIG. 4.—Sensitivities (dx_i^*/dz_j) of phosphorus pool sizes to changes in phosphorus inputs for Tuesday Lake in the summers of 1984 and 1986. Each panel shows the sensitivity of one pool to changes in input rates to all pools. *A*, dissolved P; *B*, seston; *C*, zooplankton; *D*, *Chaoborus; E*, planktivores; *F*, piscivores. Inputs: *P*, dissolved P; *S*, seston; *Z*, zooplankton; *Ch, Chaoborus; Pl*, planktivorous fish; *Ps*, piscivorous fish.

DISCUSSION

Most quantitative analyses of resilience and resistance of an ecosystem will rely on mean values of seasonally fluctuating variates. We are well aware that substantial variances may be associated with some of the parameter estimates reported here. Some parameters depend on chains of assumptions or calculations, so that errors may accumulate. While these problems occur in parameter estimates for most nutrient cycling models, it is important to acknowledge the uncertainties in the values reported here. We will focus on the differences that are so large or consistent that they are not likely to be an artifact of the variability in the data. These include four main observations: (1) phosphorus turnover rate and ecosystem resilience are positively related; (2) ecosystem resilience is greater in the shorter, planktivore-dominated food web; (3) phosphorus inputs by littoral feeding of fishes are similar in magnitude to those from hydrologic and physical processes; and (4) the seston compartment, unlike all other compartments, is more resistant to changes in phosphorus input in the piscivore-dominated food web.

DeAngelis et al. (1989*a*, 1989*b*) suggested that turnover rate of limiting nutrients is a useful empirical index of ecosystem resilience. Our data corroborate their suggestion. Analyses of nutrient turnover rate and resilience lead to the same conclusions about changes in Tuesday Lake.

Our results support the conjecture of Pimm and Lawton (1977) that longer food chains are less resilient. While resilience might increase with increasing food chain length under certain circumstances (DeAngelis et al. 1989*b*), this was not the case in Tuesday Lake. In a later article, DeAngelis et al. (1992) pointed out that slow dynamics of the top carnivore could cause resilience to decline in longer food chains. That argument applies to lake food chains in which fishes are the top predators.

In Tuesday Lake, the relationship among phosphorus turnover time (inverse of turnover rate), resilience, and food chain length is explained by the fact that the piscivore compartment has a much longer phosphorus turnover time (204 d) than the planktivore compartment (26 d in 1984, 81 d in 1986). Adding a trophic level adds a slow compartment to the system that increases phosphorus turnover time and increases the amount of time required to recover from disturbance. In aquatic systems, body size and generation time (and potentially turnover time) are often greater at higher trophic levels. In terrestrial systems the reverse is often true. It would be very interesting to compare the effects of food chain length on resilience of aquatic and terrestrial systems.

Phosphorus transfer to the pelagic zone via littoral feeding of fishes is an important flux in Tuesday Lake. Fishes represent a large phosphorus pool with relatively slow dynamics that strongly constrains phosphorus cycling rates (Kitchell et al. 1979). Many fish populations range from inshore to offshore habitats and participate in both pelagic and littoral phosphorus cycles daily (Baumann and Kitchell 1974; Brandt et al. 1980; Post and McQueen 1988) and seasonally (Wells 1968). Our results show that littoral feeding by fishes is a significant phosphorus input for the pelagic zone, that excretion by fishes is a major source of dissolved phosphorus, and that phosphorus pool sizes at lower trophic levels are sensitive to dynamics of the fish phosphorus compartment.

Similar evidence for the relative importance of phosphorus transfer by fishes from the littoral to pelagic zones in lakes was presented by Braband et al. (1990). Seasonal P excretion by roach, *Rutilus rutilus,* exceeded P inputs from the watershed but was only one-tenth of that from zooplankton. They considered P excreted by roach as "new" epilimnetic P transferred by fish from littoral areas. Lamarra (1975) presented evidence that a littoral-feeding benthophagous fish, *Cyprinus carpio,* could contribute substantially to internal phosphorus loading. Nakashima and Leggett (1980) estimated that P excretion by zooplankton was substantially greater than that by fish, but they did not discuss the origin of the P supplied by fish excretion. In enclosure experiments in lakes, effects of fish on algal production have sometimes been attributed to phosphorus inputs associated with fish. Threlkeld (1987) proposed that some of these effects were artifacts of P release from dead fish. In another mesocosm experiment, P excretion by living fish was approximately equal to that by zooplankton (Vanni and Findlay 1990). Direct measurements of the P recycling rate in enclosures have shown significant effects of fishes (Mazumder et al. 1988).

In marine systems, fish that feed nocturnally in sea grass beds and spend the day over coral heads are a major source of nutrient inputs to coral reefs (Meyer et al. 1983). Diel migrations by midwater-feeding marine fish that move nocturnally to rocky reefs have also been proposed as an important source of carbon (Bray et al. 1981). Seasonal migrations by anadromous fish such as salmon and alewives provide major inputs of nutrients to coastal lakes and streams (Krokhin 1967; Durbin et al. 1979).

The trophic cascade hypothesis for lakes was developed to explain variations in primary production that cannot be attributed to inputs of the limiting nutrient, which is usually phosphorus (Carpenter et al. 1985). Variations in fish community structure alter zooplankton communities and herbivory, causing algal biomass and production to deviate from expectations based on nutrient input alone. The trophic cascade is usually framed in terms of population or trophic level interactions. However, if the trophic cascade is consistent with nutrient cycling concepts, then it should be possible to express it in terms of nutrient dynamics.

The changes in trophic structure that derive from trophic cascades can be viewed as changes in the phosphorus cycle driven by fishes. A basic expectation of the trophic cascade hypothesis is that piscivore-dominated food chains exhibit less algal biomass per unit nutrient input than do food chains dominated by planktivores (Carpenter et al. 1985). Our data support this idea: size of the seston pool (which consists mainly of algal phosphorus) was both smaller and less sensitive to phosphorus inputs when the food web was dominated by piscivores rather than planktivores. Lower sensitivity of primary producers to changes in nutrient input is a dynamic property of the piscivore-dominated food web. Seston phosphorus is transferred to higher trophic levels or lost from the system at a relatively rapid rate. In the planktivore-dominated web, in contrast, phosphorus tends to accumulate in the seston.

Biomanipulation, the restructuring of fish communities to improve water quality (Shapiro et al. 1975; Gulati et al. 1990; Kitchell 1992), can also be viewed from the perspective of the phosphorus cycle. Shapiro and Wright (1984) found losses of seston phosphorus consistent with our model after biomanipulation of Round Lake, Minnesota. Like the trophic cascade theory, biomanipulation has traditionally been explained in population and community terms. However, from a lake management viewpoint, it does not matter whether changes in algal biomass are explained by changes in predation or phosphorus cycling. Both perspectives are equally valid.

The equilibrium analysis in this article contrasts with the usual view of the trophic cascade as a transient, nonequilibrium phenomenon (Carpenter and Kitchell 1987, 1988). Biomanipulations, or management applications of the trophic cascade to improve water quality, may require sustained management of fish stocks to maintain the desired nonequilibrial conditions (Gulati et al. 1990; Kitchell 1992). Our analysis implies that the trophic cascade may have stronger effects on phosphorus dynamics under nonequilibrium conditions than at equilibrium. Transient, nonequilibrium effects of increasing piscivores may include reduced phosphorus recycling by fishes, increased net flow of phosphorus into fishes, and decreased amounts of phosphorus in the water, seston, and zooplankton. While these differences were less pronounced at equilibrium, the piscivore-dominated system still had lower phosphorus recycling rates and less phosphorus in seston (2.0 vs. 7.6 μg/L). The piscivore-dominated system also had lower resilience (i.e., recovered more slowly after perturbation). This slow response is explained by the relatively slow growth of the piscivores, which are the major phosphorus pool of the system. Seston concentrations were more resistant (less sensitive) to phosphorus inputs in the piscivore-dominated system than in the planktivore-dominated system.

Our analysis cannot address the resistance of seston concentrations to phosphorus inputs under nonequilibrium conditions. However, nonequilibrium analyses of more realistic, nonlinear models imply that phytoplankton concentrations may be more resistant to variations in phosphorus input in piscivore-dominated systems (Carpenter and Kitchell 1987; DeAngelis et al. 1989*b;* Carpenter 1992; Carpenter et al. 1992; Vanni et al. 1992). Some whole-lake experiments and comparative studies also suggest that algae in piscivore-dominated systems may be more resistant to fluctuations in nutrient input (Gulati et al. 1990; Carpenter et al. 1991). Nevertheless, the question of how food web configuration affects algal resistance to nutrient inputs under nonequilibrium conditions remains an important one for aquatic ecology.

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LITERATURE CITED

Baumann, P. C., and J. F. Kitchell. 1974. Diel patterns of diet and feeding of bluegill (*Lepomis macrochirus*) in Lake Wingra, Wisconsin. Transactions of the American Fisheries Society 103:255–260.

Braband, A., B. A. Faafeng, and J. P. M. Nilssen. 1990. Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. Canadian Journal of Fisheries and Aquatic Sciences 47:364–372.

Brandt, S. B., J. J. Magnuson, and L. B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 37:1557–1564.

Bray, R. N., A. C. Miller, and G. G. Geesey. 1981. The fish connection: a trophic link between planktonic and rocky reef communities? Science (Washington, D.C.) 214:204–205.

Carpenter, S. R. 1992. Destabilization of planktonic ecosystems and blooms of blue-green algae. Pages 461–482 *in* J. F. Kitchell, ed. Food web management: a case study of Lake Mendota. Springer, New York.

Carpenter, S. R., and J. F. Kitchell. 1987. The temporal scale of variance in limnetic primary production. American Naturalist 129:417–433.

———. 1988. Consumer control of lake productivity. BioScience 38:764–769.

———, eds. In press. The trophic cascade in lake ecosystems. Cambridge University Press, Cambridge.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.

Carpenter, S. R., M. M. Elser, and J. J. Elser. 1986. Chlorophyll production, degradation, and sedimentation: implications for paleolimnology. Limnology and Oceanography 31:112–124.

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 1987. Regulation of lake primary productivity by food web structure. Ecology 68:1863–1876.

Carpenter, S. R., P. R. Leavitt, J. J. Elser, and M. M. Elser. 1988. Chlorophyll budgets: response to food web manipulation. Biogeochemistry 6:79–90.

Carpenter, S. R., T. M. Frost, J. F. Kitchell, T. K. Kratz, D. W. Schindler, J. Shearer, W. G. Sprules, M. J. Vanni, and A. P. Zimmerman. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems. Pages 67–96 *in* J. Cole, S. Findlay, and G. Lovett, eds. Comparative analyses of ecosystems: patterns, mechanisms, and theories. Springer, New York.

Carpenter, S. R., B. Johnson, C. Luecke, C. P. Madenjian, J. Post, L. G. Rudstam, M. J. Vanni, X. He, Y. Allen, R. Dodds, K. McTigue, and D. Schael. 1992. Modeling the Lake Mendota ecosystem: synthesis and evaluation of progress. Pages 451–460 *in* J. F. Kitchell, ed. Food web management: a case study of Lake Mendota. Springer, New York.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology 14:215–230.

Clady, M. D. 1974. Food habits of yellow perch, smallmouth bass and largemouth bass in two unproductive lakes in northern Michigan. American Midland Naturalist 91:453–459.

Cole, J., N. F. Caraco, and G. E. Likens. 1990. Short-range atmospheric transport: a significant source of phosphorus to an oligotrophic lake. Limnology and Oceanography 35:1230–1237.

Cressa, C., and W. M. Lewis, Jr. 1986. Ecological energetics of *Chaoborus* in a tropical lake. Oecologia (Berlin) 70:326–331.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. International Vereinigung für theoretische und angewandte Limnologie, Mittelungen 18:1–151.

Davis, J. A., and C. E. Boyd. 1978. Concentrations of selected elements and ash in bluegill (*Lepomis macrochirus*) and certain other freshwater fish. Transactions of the American Fisheries Society 107:862–867.

DeAngelis, D. L., P. J. Mulholland, A. V. Palumbo, A. D. Steinman, M. A. Huston, and J. W. Elwood. 1989*a*. Nutrient dynamics and food web stability. Annual Review of Ecology and Systematics 20:71–95.

DeAngelis, D. L., S. M. Bartell, and A. L. Brenkert. 1989*b*. Effects of nutrient recycling and food-chain length on resilience. American Naturalist 134:778–805.

DeAngelis, D. L., P. J. Mulholland, A. L. Steinman, and A. V. Palumbo. 1992. Nutrient limitation and the structure of food webs. Proceedings of the Yokohama Intecol Meeting (in press).

Durbin, A. G., S. W. Nixon, and C. A. Oviatt. 1979. Effects of the spawning migration of the alewife, *Alosa pseudoharengus,* on freshwater ecosystems. Ecology 60:8–17.

Elser, J. J., and S. R. Carpenter. 1988. Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. Oecologia (Berlin) 76:148–154.

Elser, J. J., M. M. Elser, N. A. MacKay, and S. R. Carpenter. 1988. Zooplankton-mediated transitions between N and P limited algal growth. Limnology and Oceanography 33:1–14.

Elser, M. M., C. N. von Ende, P. Soranno, and S. R. Carpenter. 1987. *Chaoborus* populations:

response to food web manipulations and potential effects on zooplankton communities. Canadian Journal of Zoology 65:2846–2852.

Grodzinski, W., R. Z. Klekowski, and A. Duncan. 1975. Methods for ecological bioenergetics. Blackwell, Oxford.

Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer, and E. van Donk, eds. 1990. Biomanipulation: tool for water management. Kluwer Academic, Dordrecht.

Hallam, T. G., R. R. Lassiter, J. Li, and L. A. Suarez. 1990. Modelling individuals employing an integrated energy response: application to *Daphnia*. Ecology 71:938–954.

Hamilton, J. G., and P. M. Powles. 1979. Feeding habits and growth of young-of-the-year largemouth bass (*Micropterus salmoides*) near its northern limit, Nogies Creek, Ontario. Canadian Journal of Zoology 57:1431–1437.

Harrison, G. W., and S. Fekete. 1980. Resistance of nutrient cycling systems to perturbations of the flow rates. Ecological Modelling 10:227–241.

He, X. 1986. Population dynamics of northern redbelly dace (*Phoxinus eos*), and central mudminnow (*Umbra limi*), in two manipulated lakes. Masters thesis. University of Wisconsin—Madison, Madison, Wisc.

Hodgson, J. R., and J. F. Kitchell. 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). American Midland Naturalist 118:323–336.

Holling, C. S. 1973. Resilience and stability in ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Keast, A. 1985. Development of dietary specializations in a summer community of juvenile fishes. Environmental Biology of Fishes 13:211–224.

Keast, A., and J. M. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Transactions of the American Fisheries Society 114:204–213.

Kitchell, J. F., ed. 1992. Food web management: a case study of Lake Mendota. Springer, New York.

Kitchell, J. F., R. V. O'Neill, D. Webb, G. W. Gallepp, S. M. Bartell, J. F. Koonce, and B. S. Ausmus. 1979. Consumer regulation of nutrient cycling. BioScience 29:28–34.

Krokhin, E. M. 1967. Influence on the intensity of passage of the sockeye salmon (*Oncorhynchus nerka*) on the phosphate content of spawning lakes. Fisheries Research Board of Canada Translation Series 417. 15:26–31.

Lamarra, V. A. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen 19:2461–2468.

Leavitt, P. R., and S. R. Carpenter. 1990. Regulation of carotenoid sedimentation by herbivory and photo-oxidation. Canadian Journal of Fisheries and Aquatic Sciences 47:1166–1176.

Lehman, J. T. 1980. Release and cycling of nutrients between planktonic algae and herbivores. Limnology and Oceanography 25:620–632.

Mazumder, A., D. J. McQueen, W. D. Taylor, and D. R. S. Lean. 1988. Effects of fertilization and planktivorous fish (yellow perch) predation on size distribution of particulate phosphorus and assimilated phosphate: large enclosure experiments. Limnology and Oceanography 33:421–430.

Meyer, J. L., E. T. Schultz, and G. S. Helfman. 1983. Fish schools: an asset to corals. Science (Washington, D.C.) 220:1047–1049.

Nakashima, B. S., and W. C. Leggett. 1980. The role of fishes in the regulation of phosphorus availability in lakes. Canadian Journal of Fisheries of Aquatic Sciences 37:1540–1549.

Peters, R. H., and F. H. Rigler. 1973. Phosphorus release by *Daphnia*. Limnology and Oceanography 18:821–839.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature (London) 307:321–326.

Pimm, S. L., and J. H. Lawton, 1977. The number of trophic levels in ecological communities. Nature (London) 268:329–331.

Post, J. R., and D. J. McQueen. 1988. Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): a response to prey or predators? Canadian Journal of Fisheries and Aquatic Sciences 45:1820–1826.

Reynolds, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge.

Rice, J. A., J. E. Breck, S. M. Bartell, and J. F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environmental Biology of Fishes 9:263–275.

Shapiro, J., and D. I. Wright. 1984. Lake restoration through biomanipulation: Round Lake, Minnesota the first two years. Freshwater Biology 14:371–383.

Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration. Pages 85–96 *in* P. L. Brezonik and J. L. Fox, eds. Water quality management through biological control. University Presses of Florida, Gainesville.

Swift, M. C. 1976. Energetics of vertical migration in *Chaoborus trivittatus* larvae. Ecology 57: 900–914.

Threlkeld, S. T. 1987. Experimental evaluation of trophic cascade and nutrient mediated effects of planktivorous fish on plankton community structure. Pages 161–173 *in* W. C. Kerfoot and A. Sih, eds. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, N.H.

Vanni, M. J., and D. L. Findlay. 1990. Trophic cascades and phytoplankton community structure. Ecology 71:116–124.

Vanni, M. J., S. R. Carpenter, and C. Luecke. 1992. A simulation model of the interactions among nutrients, algae, and zooplankton in Lake Mendota. Pages 427–450 *in* J. F. Kitchell, ed. Food web management: a case study of Lake Mendota. Springer, New York.

Webster, J. R ., and B. C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecological Monographs 49:51–72.

Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish and Wildlife Service Fisheries Bulletin 67:1–15.

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