1. Research Category and Sorting Code: Understanding Ecological Thresholds in Aquatic Systems through Retrospective Analysis, 2004-STAR-K2

2. Title: **Eutrophication Thresholds -- Assessment, Mitigation and Resilience in Landscapes and Lakes**

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5. Project Period: 1 July 2005 to 30 June 2007

6. Project Cost: $299,999

7. Project Summary: Eutrophication, a persistent environmental problem characterized by turbid water, toxic algae, fish kills, waterborne disease, and loss of aquatic ecosystem services, may be related to important thresholds in the phosphorus (P) cycle. We will address two main questions: (1) What thresholds in the transport and recycling of P in linked terrestrial-aquatic ecosystems cause lakes to switch between clear-water and eutrophic states? (2) How can thresholds for transport and recycling of P be manipulated to mitigate eutrophication, or increase resilience of clear water lakes against eutrophication? The research will conduct a retrospective analysis of the Yahara watershed and its major lakes (near Madison, Wisconsin), using a substantial historical data base of land characteristics and limnology. Changes in this watershed-lake system are emblematic of those in many agricultural, urbanizing regions of the United States. Approaches include statistical analyses of three different types of lake models and simulation studies using a Terrestrial-Aquatic P model. The project will describe thresholds related to eutrophication with respect to landscape, biogeochemical, and statistical characteristics. We will (1) establish whether the thresholds are likely to produce important changes in eutrophication, (2) determine how key controlling variables such as climate, landscape characteristics, land use/cover change, agricultural practices, and management actions affect thresholds, (3) evaluate prospects for mitigating eutrophication through interventions that utilize thresholds, and (4) assess changes in controlling variables that would increase or decrease resilience of clear-water and eutrophic regimes. Better understanding of thresholds related to eutrophication is a prerequisite for correcting this persistent problem in order to improve ecosystem condition, human health, and livelihoods.

8. Supplemental Keywords: soil, sediments, risk, health effects, ecological effects, bioavailability, vulnerability, susceptibility, cumulative effects, chemicals, toxics, pathogens, indicators, restoration, scaling, Bayesian, ecology, physics, environmental chemistry, modeling, Midwest, Wisconsin, WI, EPA Region 5.

OBJECTIVES

Eutrophication of aquatic ecosystems -- a prominent and problematic ecological "*regime shift*" -- affects the health and livelihoods of more than two billion people worldwide (Millennium Ecosystem Assessment in preparation for 2005 publication-a). Eutrophication is characterized by high concentrations of total phosphorus (P) and other nutrients, blooms of cyanobacteria (including some toxic varieties), oxygen depletion, fish kills, waterborne disease, and other human health problems. Over-enrichment with P is the most common cause of eutrophication of lakes and reservoirs (Schindler 1977, Smith 1998). Annual economic losses from eutrophication in the United States are estimated to be roughly \$100 billion (Costanza 1997, Postel and Carpenter 1997, Wilson and Carpenter 1999), but this is likely an underestimate because valuation studies rarely include all of the ecosystem services of fresh water (Postel and Carpenter 1997, Millennium Ecosystem Assessment 2003). Although the basic causes of eutrophication have been understood for decades, it remains a severe environmental problem that has proven difficult to ameliorate.

Eutrophication by nonpoint P pollution involves a series of steps along the hydrologic flow path from uplands, through riparian corridors, wetlands and streams, to lakes and reservoirs (Schlesinger 1997, Carpenter et al. 1998, Reed-Andersen et al. 2000, Sharpley 2002). P enters the watershed through fertilizer application, atmospheric deposition or weathering. A given P atom may cycle many times between biota and soil -- through plant uptake and decomposition, or plant uptake followed by grazing and deposition of manure, for example. P leaves the watershed in the form of crops, animal products, migrating animals, or transport by wind or water (Bennett et al. 1999). Once P enters a stream, it may spiral slowly, or in some cases (e.g. flood pulses) be transported rapidly downstream (Newbold et al. 1981, Mulholland et al. 1990, Correll et al. 1999). In lakes and reservoirs, P cycles between sediments, overlying water, and biota, producing clear water or turbid water depending on the amount of P and controls of phytoplankton growth (Scheffer 1997, Smith 1998, Kalff 2002).

Persistence of eutrophication may be related to important *ecological thresholds* and the existence of *multiple regimes* within a lake (Figure 1) (Carpenter 2003, Scheffer and Carpenter 2003, Steffen 2004). A lake may remain in a clear (desirable) regime if total P or algae remain below a threshold; once passed, the lake

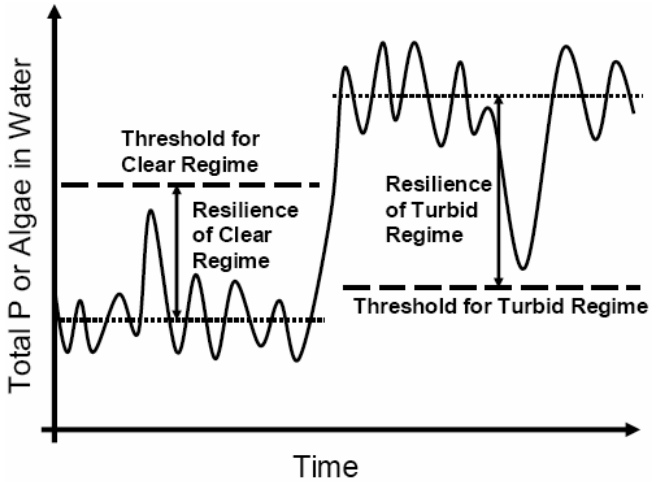

Figure 1. Eutrophication as a regime shift (Carpenter 2003). Solid fluctuating line shows the concentration of total P or algae in the water. Dotted lines show the means for the clear-water and turbid (eutrophic) regimes. Dashed lines show the thresholds for each regime. Resilience is the distance from the mean of a regime to its threshold. A resilient regime can withstand a large perturbation without switching to the other regime.

switches to the eutrophic regime, which is also stable over a range of conditions. Such a change in ecosystem conditions is often called a *regime shift* (Scheffer et al. 2001, Carpenter 2003). Returning to the clear regime requires a substantial reduction in total P or algae to cross a lower threshold (Figure 1). As a result, reversing eutrophication is slow, expensive, or sometimes impossible once the lake has shifted to the turbid regime. Knowledge of these thresholds is absolutely essential in order to maintain the lake in its desirable, clear-water state.

Eutrophic lakes have often responded slowly, or failed to respond, to mitigation of P inputs (Sas and Ahlgren 1989, National Research Council 1992, Cooke et al. 1993, Carpenter et al. 2003). ***Within-lake processes may create thresholds in the P cycle, which may explain the persistence of eutrophy***. Several internal mechanisms can create these thresholds (Carpenter 2003):

> (1) Food webs with high rates of fish harvest, low biomass of piscivores, high biomass of planktivorous fishes, and small-bodied zooplankton maintain low rates of grazing on phytoplankton and high rates of P recycling from consumers (Scheffer 1997, Carpenter et al. 2001, Lathrop et al. 2002, Sterner and Elser 2002, Beisner 2003).
>
> (2) In lakes that do not thermally stratify, the loss of macrophytes (rooted aquatic plants) allows currents to resuspend sediments, thereby mixing P into the water and maintaining high concentrations of algae (Scheffer 1997, Jeppeson et al. 1998).
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> (3) In stratified lakes, enrichment stabilizes eutrophication through rapid recycling of P (Carpenter et al. 1999, Carpenter 2003). As productivity increases, decay of sinking phytoplankton depletes oxygen, creating biogeochemical conditions that accelerate release of P from sediments (Mortimer 1941, 1942, Nürnberg 1984, Caraco et al. 1991, Nürnberg 1998, Nürnberg and LaZerte 2004).

Thus, thresholds in the recycling of P within lakes or reservoirs will be associated with both physical features of the lake and structure of the aquatic community.

Thresholds related to the movement of P from terrestrial to aquatic ecosystems may also influence the lake regime. In many agricultural regions, soil P concentrations have increased as a result of fertilizer and manure application (Bennett et al. 2001). At certain thresholds, wetlands and upland soils switch from retaining P to releasing soluble P to soil water, groundwater, or runoff (Heckrath et al. 1995, Richardson and Qian 1999). These thresholds in soil P may determine whether a given site is a P source or sink. Sites of P retention versus release are spatially variable across agricultural landscapes (Sharpley et al. 1993, Sharpley 1995, Pionke et al. 1997, Sharpley et al. 2001), and thresholds in the spatial connectivity of source vs. sink sites may also influence lake phosphorus loading and eutrophication. Thus, thresholds in the storage and runoff of P in the terrestrial landscape will be associated with the spatial and temporal patterns of past and current land use / land cover, as well as climate, soil properties and topography (National Research Council 1992, Weller et al. 1998, Bennett et al. 1999, Revenga et al. 2000, Wickham et al. 2000, Bennett et al. 2001, Reed-Andersen and Carpenter 2002, Wickham et al. 2002).

Despite the substantial mechanistic understanding of eutrophication, the ability to assess and predict thresholds, as well as to manipulate ecosystems in relation to thresholds, is quite limited. Potentially, one could manage eutrophication by preventing ecosystems from crossing certain thresholds. For example, ***P loads could be held below the threshold that triggers eutrophication***. Alternatively, the ***thresholds could be altered so that ecosystems are less likely to cross them***. Lake management techniques such as hypolimnetic aeration, alum treatment, or biomanipulation attempt to change thresholds (Cooke et al. 1993, Carpenter et al. 1999). ***Nevertheless, it is remarkably difficult to determine whether thresholds exist, quantify them, identify key controlling variables, and determine how to avoid them or manipulate them to mitigate eutrophication***. These limitations derive from lack of appropriate models and methods for inference, as well as lack of data.

Here we propose to quantify thresholds in the terrestrial and aquatic P cycle that affect eutrophication, and assess the effects of management interventions on the thresholds and eutrophication. This research will emphasize new models and methods for inference to address two overarching questions:

Question 1: What thresholds in the transport and recycling of P in linked terrestrial-aquatic ecosystems cause lakes to switch between clear-water and eutrophic states?

First, we will analyze long-term data on watersheds and lakes to characterize the within-lake biogeochemical mechanisms and key controls on thresholds for recycling of P from lake sediments, and the flux of P to aquatic primary producers in lakes. Next, we will integrate these results with a spatially explicit terrestrial-aquatic simulation model to characterize the spatial thresholds affecting retention or release of P across landscapes, and the transport of P from terrestrial to aquatic ecosystems.

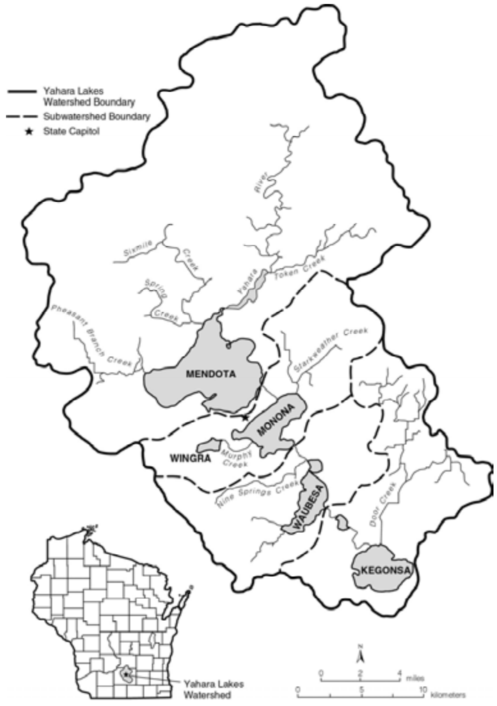

Figure 2. Yahara Watershed and its major lakes (from Lathrop 1992).

Question 2: How can thresholds for transport and recycling of P be manipulated to mitigate eutrophication, or increase the resilience of clear-water lakes to eutrophication?

We will identify the key controlling variables for thresholds that affect eutrophication and explore the ways in which eutrophication can best be mitigated or prevented. We will explore responses to climate, land use, and management interventions using the integrated terrestrial-aquatic model to simulate the hydrology, P dynamics and water quality of the Yahara watershed and its five lakes.

Study Area: The Yahara Watershed and Lakes

We will conduct an analysis of eutrophication thresholds, building upon the substantial historical data base for the Yahara watershed (near Madison, Wisconsin, USA: 43˚6'N, 89˚24'W). The system drains 996 km^2 and contains 5 major lakes (Figure 2 and Table

1). The watershed's land use is largely agricultural, with urbanized areas and some remnant native vegetation. Agriculture has dominated the landscape through most of the 20th century, but current land-use changes reflect increasing suburban development.

The Yahara watershed is representative of many agriculture-dominated landscapes subject to urban and suburban development in the U.S. (Turner et al. 1998). P loads from nonpoint runoff substantially exceed those that occurred prior to European agriculture (Soranno 1996). Furthermore, groundwater extraction, reduced infiltration, and increased runoff from impervious surfaces have significantly altered the hydrology of the lakes (Soranno 1996, Wegener 2001). Species invasions and changes in the fishery have altered grazing and the frequency of algal blooms (Kitchell 1992, Lathrop et al. 2002). Similar changes are known for many watersheds of the U.S. and other OECD nations (Millennium Ecosystem Assessment in preparation for 2005 publication-a).

The Yahara lakes and watershed have been studied extensively for more than a century. From the wealth of ecological data available for this watershed-lake system (Brock 1985, Kitchell 1992, Lathrop et al. 2002), we will focus on data collected since 1976 by the Wisconsin Department of Natural Resources and the North Temperate Lakes Long-Term Ecological Research program funded by NSF (http://lter.limnology.wisc.edu). Available spatial data sets include digital elevation, soils, weather data, land use / land cover (historical and contemporary), riparian vegetation, and maps of each lake's bathymetry. Limnological data include temperature/oxygen profiles, nutrients (TP, SRP, TN, NO_3, NH_4), DOC, ion balances, chlorophyll, phyto- and zooplankton counts, fish abundance, and macrophyte distribution.

Table 1. Characteristics of the 5 main Yahara lakes. Total P, total N from spring mixis; ANC from spring and fall mixis; chlorophyll (surface) from open water season. Source: North Temperate Lakes LTER, http://lter.limnology.wisc.edu.

Lake	Watershed Area (km²)	Lake Area (ha)	Mean Depth (m)	ANC (µeq/L)	Total P (µg/l)	Total N (µg/l)	Chlorophyll (µg/l)
Wingra	22	140	2.7	3736	32.3	932	10.3
Mendota	602	3938	12.8	3692	103	814	6.7
Monona	720	1324	8.2	3404	78	866	9.2
Waubesa	842	843	4.7	3500	50.9	610	13.1
Kegonsa	996	1299	5.1	3600	46.9	770	12

APPROACH

Multiple models and methodologies are needed to assess the behavior of thresholds within ecosystems (Carpenter 2003, Scheffer and Carpenter 2003). Our approach employs two main strategies: (1) **statistical analysis of long-term lake data**, and (2) analysis of an integrated **terrestrial-aquatic phosphorus model** to explore linked landscape-lake biogeochemical and ecological processes. Both elements rely on existing data and the adaptation of existing modeling frameworks to the Yahara watershed-lake ecosystem.

First, our statistical analysis will employ long-term (since 1976) limnological data and three complementary types of models of within-lake P processing. We will assess the evidence for existence of eutrophication thresholds in the each of the five Yahara lakes, and test for mechanisms related to lake eutrophication and internal processes leading to thresholds (thereby addressing part of Question 1). Results of the retrospective analysis will also be used in the calibration and validation of the integrated terrestrial-aquatic phosphorus model.

Second, we will develop a spatially explicit, integrated terrestrial-aquatic phosphorus model that includes: (i) a mechanistic within-lake eutrophication model (derived from the statistical analysis); and (ii) a generalized mass transport framework to simulate the movement of water and P across the landscape and into (and between) lakes. Numerical experiments with this integrated simulation model will characterize the terrestrial and aquatic thresholds for P transport and recycling, addressing the remaining portions of Question 1. The integrated model will also be used to assess spatial and temporal controls on eutrophication thresholds and to explore simulations wherein key control variables are manipulated; these simulations and sensitivity analyses will address Question 2.

Within-Lake Modeling Using Long-term Limnological Data (Question 1)

We will explore in-lake processing of phosphorus using statistical analyses of long-term ecological datasets, to test for and characterize within-lake P recycling thresholds in each lake in the Yahara watershed. Because one of the critical challenges in testing hypotheses about thresholds is that the answer may depend on the statistical model used to describe ecosystems (Clark et al. 2001, Carpenter 2003, Scheffer and Carpenter 2003). Therefore, we will employ three different types of lake models of within-lake processing: (1) a *detailed mechanistic* lake model (Genkai-Kato and Carpenter in press); (2) a *semi-mechanistic minimal* lake model (Ludwig et al. 2003); and (3) a purely *descriptive statistical* lake model (Carlin et al. 1992, Stephens 1994). These three types of lake models represent different tradeoffs among realism, applicability to diverse lakes, and statistical tractability. We will directly compare inferences made using each of these three different lake model types, which are described below.

Lake Model A: Detailed Mechanistic

Genkai-Kato and Carpenter (in press) developed a detailed lake model to address the response of eutrophication thresholds to lake morphometry, macrophyte cover, temperature and food web structure. Applicable to a diverse range of lakes and conditions, the model represents key limnological mechanisms and established empirical relationships. Although the model contains a relatively large number of parameters, the equations can be parameterized for the Yahara lakes by utilizing the decades of data available on P loading, P stocks, macrophytes and grazers. To apply the model for this region, we will expand its capabilities to incorporate grazing losses using existing data from the Yahara lakes and the modeling procedures of Carpenter et al. (1993) and Beisner et al. (2003).

We will conduct a Bayesian uncertainty analysis of this model, computing posterior distributions of model parameters, the thresholds for eutrophication, and resilience. Threshold levels in each of the five Yahara lakes will be examined as functions of lake attributes that cannot be manipulated easily (mean depth, thermocline depth, water temperature), and those that may be amenable to mitigation through management (P loads, macrophyte cover, and food web structure). Probability distributions of thresholds will be calculated using a Gibbs sampler from the posterior predictive distribution of the model (Casella and George 1992, Gelman et al. 1995). Results will be compared to present conditions and simulations of future conditions (described below) to assess possible future changes in thresholds, risks of eutrophication, and prospects for reducing risk of eutrophication by manipulation of variables that control thresholds.

Lake Model B: Semi-Mechanistic Minimal

Ludwig et al. (2003) presented a relatively simple semi-mechanistic model for dynamics of water and sediment phosphorus in stratified lakes. In P-limited lakes, nearly all the P is in organisms during the growing season -- so total P concentration in the water is a proxy for phytoplankton biomass. Detailed mechanisms related to macrophytes and morphometry are not represented explicitly, but are instead parameterized statistically. Though this model is less mechanistic than Lake Model A, it retains key mechanisms for stratified lakes and reservoirs and is more tractable statistically due to the smaller number of parameters. Furthermore, previous research has analyzed this model in an economic cost/benefit decision framework (Carpenter et al. 1999, Ludwig et al. 2003). As a result our statistical analyses will be directly applicable to economic decision analyses under uncertainty, an important consideration for the practical manipulation of factors influencing lake thresholds.

Preliminary analysis with this lake model indicates substantial risk that Lake Mendota (the largest of the Yahara lakes) will cross the load threshold to a eutrophic state that is difficult to reverse (Figure 3). It also indicates that this risk will increase if loads are increased beyond the range observed so far. While P loads are sufficient low, this model exhibits two locally stable regimes, a clear-water regime and a turbid regime, separated by a P threshold (Carpenter 2003). When the load threshold is exceeded, the clear-water regime no longer exists and the lake will remain in the turbid (eutrophic) regime until the P load drops below the load threshold and the sediment P is depleted -- a reversal that would likely take decades. Lake Mendota appears to be on the cusp of crossing the load threshold. If this occurs, its P concentration and rate of export of P to downstream lakes will also increase. This may cause other lakes to cross their P load thresholds as well, because upstream lakes are major P sources for downstream lakes: Lake Mendota is the largest P source for Lake Monona, which is a large P source for Lake Waubesa, which is a large P source for Lake Kegonsa.

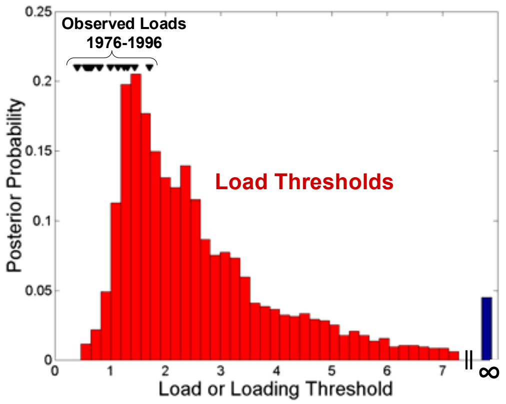

Figure 3. Posterior probability distribution for the loading threshold (g P m-2 y-1) for Lake Mendota. Triangles indicate observed annual loads, 1976-1996. The distribution was computed using a Gibbs sampler (Gelman et al. 1995) from the posterior distribution presented by Carpenter (2003). Observed loads were presented by Lathrop et al. (1998).

Note that the distribution of resilience (as defined in Figure 1) could be computed from the same information used to compute Figure 3. The resilience of a given regime is the difference between the mean state of the regime and the system threshold (Carpenter et al. 2001). We will extend our analysis to compute the distributions of resilience for both clear-water and eutrophic states for each of the Yahara lakes.

Historical P budget data (from 1976-2004) will be analyzed for the three thermally stratified lakes in the Yahara chain (Mendota, Monona and Waubesa) using the lake model of Ludwig et al. (2003). Priors will be drawn from published data (Carpenter 2003) and likelihoods will be calculated from the observed loads and P masses in the lake; posterior distributions will be studied using a Gibbs sampler (Gelman et al. 1995). Results will include posterior distributions for model parameters, the P threshold, and the load threshold. This analysis will go substantially beyond previous studies, which have focused only on parameter distributions and been limited to data from a shorter time period (1976-1996) in only one lake (Mendota) (Figure 3).

Lake Model C: Descriptive Statistical

Bayesian switchpoint methods (Carlin et al. 1992, Stephens 1994) can be used to determine posterior probability distributions of discontinuities, including thresholds, in long-term or spatially extensive datasets. Switchpoint methodologies have been expanded and several variants have been applied to environmental thresholds, including thresholds in the P cycle (Richardson and Qian 1999, Qian et al. 2003, Qian et al. 2004). Like more familiar statistical models, such as regressions, the parameters of Bayesian switchpoint models do not necessarily represent any ecological parameter. Although the parameters are abstract, Bayesian switchpoint models are well understood statistically. In some, cases the posterior distributions have well-understood (or even analytic) solutions. Thus Bayesian switchpoint models are tractable statistically, even though the parameters may not always have simple ecological interpretations.

Bayesian switchpoint models will be used to examine the posterior distributions of thresholds in time-series observations from all 5 Yahara lakes. Initially we will focus on chlorophyll and total P to facilitate comparisons with the models described above. In these analyses, a broad, flat probability distribution for a threshold indicates that the threshold is poorly defined, whereas a narrow, tall probability distribution indicates that the threshold is well defined.

In addition, we will analyze time series for oxygen depth profiles to characterize thresholds in deoxygenation. Depletion of oxygen from the hypolimnion is associated with increased recycling of P (Nürnberg 1984, 1998). Thus changes in oxygen profiles may foreshadow P recycling events (Stow et al. in review).

Terrestrial-Aquatic Phosphorus Model (Questions 1 and 2)

In the second major component of our project, we will develop and use a spatially explicit simulation model of terrestrial and aquatic P storage and flow to understand the past and possible future behavior of the Yahara watershed and its lakes. The model will be built and used in two phases. First, we will focus on the storage and movement of P across terrestrial landscapes within the watershed to explore the factors influencing P delivery to lakes. Next, we will combine this spatial routing model with the detailed mechanistic lake model (Lake Model A) to produce an integrated model that simulates the watershed and all five lakes concurrently. The integrated model will allow us to: (1) determine the physical and biogeochemical thresholds that affect transport and recycling of P in linked terrestrial-aquatic ecosystems (addressing Question 1); and (2) study the effects of differing P loads and timing on lake processes within situations of changing land use / land cover, weather patterns, within-lake processes, and watershed management strategies (addressing Question 2).

Phase 1: Land-Stream P Retention, Transformation, and Transport

We will adapt and extend an existing modeling framework developed at the University of Wisconsin-Madison to analyze water and nutrient balance and movement in linked aquatic-terrestrial systems of northern temperate lakes (Cardille et al. in press). Our model has successfully simulated water flows among a series of interconnected lakes and watersheds and has been used to explore lake responses to watershed area, lake connectivity, and climate variation (Cardille et al. in press). This approach will be extended, and adapt existing models of P transport from land to lakes (e.g., Gburek and Sharpley 1998, Sharpley 2002, Wickham et al. 2002) including one that has already been applied to the Lake Mendota watershed (Soranno 1996). Like the model of Wade et al. (2002), our model will include transport and retention of P in both terrestrial and aquatic environments.

The model will simulate movement of water and phosphorus across the Yahara Watershed, to streams and stormwater systems, and to lakes using a series of nodes and connections (Figure 4, Figure 5). Nodes will represent both aquatic (e.g., a stream or lake) and terrestrial (e.g., a land use patch) entities (Figure 4), and fluxes of water and phosphorus will occur between each node. The model accommodates multiple fluxes of different rates leaving each node and connecting to any number of downstream nodes. Terrestrial nodes, which can vary in size to represent individual cells or whole parcels, will hold most accumulated phosphorus below a given threshold (Heckrath et al. 1995, Richardson and Qian 1999), releasing P to streams or groundwater via a relatively slow flux. Beyond a threshold concentration of soil P, available P will be released in rainfall-driven runoff events to streams (an intermediate-speed flux) or stormwater systems (a relatively fast flux). Streambed P will also be represented by nodes (as in Reed-Andersen et al. 2000) with the rate of P release varying with

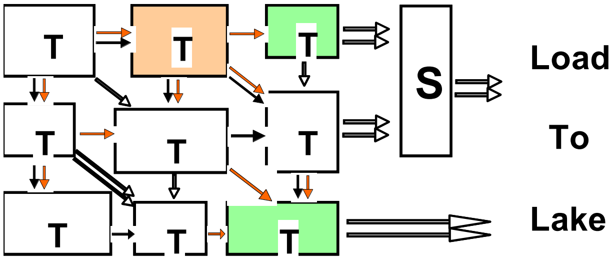

Figure 4. Land-stream P flux model to explore variation of the timing and amount of phosphorus delivered from terrestrial units (T) and stream units (S) to lakes in the Yahara watershed. Instances of each unit type behave similarly, routing P based on thresholds and connectivity in transient simulations of arbitrary duration. Terrestrial units can represent, for example, residential parcels (beige), buffer strips (green), or agriculture (unshaded "T" nodes). Characteristics of each unit (such as the size, initial phosphorus soil concentration, and management practices of a terrestrial farm parcel) may vary widely, further influencing ecosystem behavior and potential thresholds.

streamflow (Coussot 1994). Loss from or gain to labile and non-labile P pools (e.g., binding of P to soil or sediment particles, fertilizer application on land) occurs within nodes, and movement and storage among and within nodes is subject to rules of conservation of mass.

The model will be developed initially using current land-cover patterns and the topography and soils of the watershed. Contiguous cells of the same land-cover (e.g., crop fields, suburban development) and topographic position (e.g., on the same slope) will be aggregated to form the terrestrial nodes. The initial distribution of soil P concentrations will be assigned to each node based on spatially extensive empirical data for the watershed (Bennett 2003). Fluxes leaving terrestrial nodes will be donor determined, and transfer coefficients will be a function of the soil type, topography, and precipitation intensity. Threshold concentrations of soil P will be a function of soil type, topography, and land cover. Transport components will be based on ongoing EPA-funded research on P availability and transport in the Yahara watershed (directed by Dr. Richard Lathrop, a participant in this project). The model will be run on a daily time step using weather and precipitation data; most transport of P will occur following precipitation events. From this landscape network of terrestrial and stream nodes and fluxes, the model will produce a spatial depiction of P sources and sinks across the landscape, the total P loading per day that enters each of the 5 lakes, and the residence time of P in each node.

The P retention and transport model will be subjected to a standard sensitivity analysis, in which model parameters are varied +/- 10%, as well as to an uncertainty analysis using PEST software (http://www.sspa.com/pest/index.html), in which model parameters are varied across the range of values observed in the empirical data. We will then explore the effect of initial conditions and transient perturbations on the timing and amount of phosphorus delivery to Yahara lakes. We will vary the initial P amounts and spatial pattern of P on land and in streams, and the values of the threshold concentrations of soil P that produce P movement. We will determine the conditions (e.g., soil P concentrations, transfer coefficients, and precipitation intensity) under which the spatial arrangement of land-use / land-cover changes the timing and amount of P delivery to the Yahara lakes.

Phase 2: Integrated Terrestrial-Aquatic Model: Prospects for Eutrophication, Mitigation, and Resilience

The second phase of model development will be to integrate the terrestrial P retention and transport model with the within-lake models for each of the five lakes (Figure 5). The five lake nodes will be connected to terrestrial processes, streams, and the other lakes. Behavior of this integrated model will be calibrated to known P fertilizer application rates, soil P accumulation estimates, and observed within-lake P concentrations through time. The model will track the daily and annual P loads to each lake, the duration of anoxia, the resilience to eutrophication, and P stock patterns in labile and non-labile soil and lake pools. We will subject the model to a standard sensitivity analysis, in which model parameters are varied +/- 10%, as well as to an uncertainty analysis using PEST software (http://www.sspa.com/pest/index.html), in which model parameters are varied across the range of values observed in the empirical data.

We will conduct simulation experiments to explore the effects of plausible environmental changes and management interventions for the Yahara watershed using the terrestrial-aquatic P model, drawing upon previous studies indicating the major drivers in this system. We will explore the impact of the following major ecosystem drivers on threshold behaviors, eutrophication risk, and resilience to and mitigation of eutrophication. Our overarching goal is to identify the combinations of conditions that cause lakes to switch between the clear-water and eutrophic regimes.

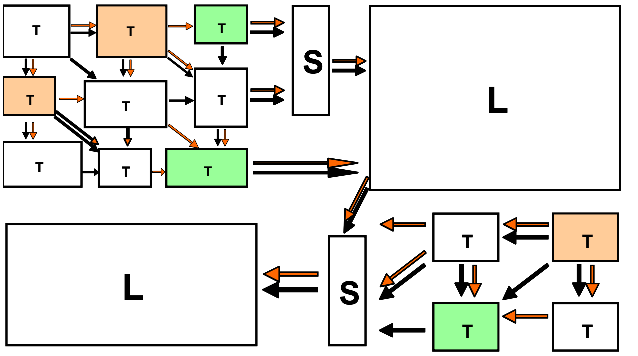

Figure 5. Terrestrial-aquatic simulation model of P movement and storage among terrestrial units (T), streams (S), and lakes (L) in the Yahara watershed. Full coupling of land, stream and lake nodes allows transient simulations tracking (1) storage and movement of P on land, (2) lake P loading and water quality response and (3) assessment of eutrophication risk and potential success of mitigations, as described in the text.

We will focus our analyses on the following drivers:

Climate: The climate of the Yahara watershed exhibits very strong seasonal and interannual variation, and includes contributions of well-known climatic phenomena (such as the El Nino – Southern Oscillation and the North Atlantic Oscillation) (Magnuson et al. 2000). We will explore how variations in climate – especially those that create extreme hydrologic events, such as the floods of 1993 or the excessive spring rainfalls of 2004 – affect the integrated terrestrial-aquatic system. A retrospective analysis of climatic statistics (from 1900 to 2004) will be performed, using various combinations of historical climate records. In addition, we will consider the possible future weather patterns of the Yahara watershed, which may differ substantially from today (Greenland et al. 2003, Hayden and Hayden 2003, Kling et al. 2003). We will perform sensitivity analyses with the integrated model following along lines of possible future climate change, including: (1) increased temperatures, particularly in spring and winter, with nighttime temperatures elevated more than day-time temperatures; (2) longer growing seasons, especially due to early onset of spring; and (3) increased frequency of extreme precipitation events while maintaining total seasonal precipitation amounts in the contemporary range.

Land Cover: Land-use/land-cover have well-know associations with water quality (e.g., Jordan et al. 1997, Carpenter et al. 1998, Jones et al. 2001, Gergel et al. 2002, Wickham et al. 2002, Strayer et al. 2003, Weller et al. 2003). For example, storm runoff in the Yahara watershed has increased since the 1930s as the region has urbanized (Wegener 2001). Phosphorus loading has also increased with development in the watershed (Soranno 1996). We will use the current land cover in each lake's watershed and a time series of three land-cover snapshots for Lake Mendota (air photo-derived 1930s and 1960s, and satellite-derived 1990s) to develop a spatially dependent Markov model of land use change (e.g., Wear et al. 1996). We will simulate the changing P load to the lakes as the landscape is converted from agricultural dominance to mixed urban, suburban, and agricultural land cover (Dane County Regional Planning Commission 1997). Changes in the 20th century will also be contrasted with pre-settlement conditions (Soranno 1996). We will then use the modeling framework to explore several alternative future patterns of development: (a) projections from the regional land-use planning commission (Dane County Regional Planning Commission. 1997); (b) minimal-growth; and (c) a pattern in which future development is sited preferentially to minimize impact on lake water quality.

Agricultural Land Use: Land-use practices, including fertilizer application, strongly affect concentrations of P in the soil in these regions (Bennett et al. 1999). We will contrast current practices with Agricultural Extension Service recommendations (Bennett et al. 1999) as well as high-animal- and low-animal-density situations. We will also conduct sensitivity analyses with increased versus decreased tiling of croplands, to investigate effects of changes in the connectivity of agricultural fields to drainage systems. We will conduct simulations with varying amounts of land assigned to Conservation Reserve, to assess the potential effects of the Conservation Reserve Program on P cycling and eutrophication.

Riparian Buffers: The spatial pattern and density of riparian buffers appear to affect nutrient loading to water bodies, in both theoretical studies (e.g., Weller et al. 1998) and field studies covering substantial areas (Baker et al. 2001, Reed-Andersen and Carpenter 2002, King et al. in press). We will conduct model analyses that vary buffer density (current buffer density vs. buffers removed vs. buffers on all stream and lake margins), as well as analyses that vary buffer arrangement (buffers of various widths arrayed for optimal to minimal cumulative retention ability).

Changes in the Food Web: In Lake Mendota, biomanipulation has been used to intensify grazing on phytoplankton and improve water clarity (Kitchell 1992, Lathrop et al. 2002). Biomanipulation alters the abundance of fish and zooplankton that graze algae (Cooke et al. 1993). In addition, invasion of zebra mussels could significantly alter grazing rates in the Yahara lakes (Reed-Andersen et al. 2000). We will perform simulations with both low and high levels of grazing losses to evaluate the potential effects of such changes in the food web on eutrophication thresholds.

Macrophytes: Historically, the Yahara lakes have exhibited a considerable range of macrophyte cover (Nichols et al. 1992, Trebitz et al. 1993, Nichols and Lathrop 1994). This is partly due to their morphometry, which ranges from shallow, unstratified Lake Wingra with its extensive macrophyte beds to deep, stratified lakes like Lake Mendota where macrophyte beds occupy less than 20% of the surface area. We will use the integrated model to investigate potential responses of macrophyte cover and possible thresholds for dominance by macrophytes versus phytoplankton.

The model simulations and sensitivity studies will be run in a factorial design that permits us to explore a wide range of possible conditions in the Yahara watershed. Because many of these sensitivity studies involve stochasticity (e.g., climate variability and the Markov process representing land use/ land cover changes), simulations will be replicated as ensembles. Eutrophy and resilience of the five Yahara lakes will be evaluated using the following measures: (a) the number of lakes that became eutrophic each year; (b) the number of lakes that reverted to a clear-water state each year; (c) for each lake, the number of years in which it became eutrophic; (d) mean duration of eutrophy across lakes; and (e) mean resilience to eutrophication through time across lakes.

Using these watershed-scale measures of resilience, along with similar values calculated for individual lakes, we will assess the resilience of each lake to major factors controlling the likelihood of crossing eutrophication thresholds, the effects of proposed mitigation strategies, and the differences between lake-specific and watershed-scale responses.

EXPECTED RESULTS AND BENEFITS

We will assess the role of thresholds for eutrophication in relation to key factors, such as climate, land use practices, hydrology, lake characteristics (morphometry, macrophytes, food web structure), and management interventions. The multidimensional complexity of these processes is a barrier to understanding and action. To summarize results in a more transparent way, we will develop graphical summaries of susceptibility to eutrophication for watershed-lake ecosystems.

As a simplified two-dimensional example, suppose that buffer pattern (continuous versus intermittent) and the relative importance of urban versus agricultural land use are considered as key factors (Figure 6). Three categories of susceptibility may emerge: a "resilient" category, in which the clear-water regime is relatively resilient to perturbations of drivers; a "permanently eutrophic" category, in which the lake(s) are already eutrophic and are likely to remain so; and a "mitigation" category, in which human actions may make eutrophication more or less likely. Within the "mitigation" category, models can be used to identify key controls. For example, under some conditions patterns of urban development may strongly affect risk of eutrophication, whereas in other conditions agricultural variables such as livestock density or cropping regime may have the most important effects (Figure 6).

Each threshold that we identify will be described in terms of landscape, biogeochemical, and statistical characteristics. In addition, we will answer several important questions related to management. Specifically, we will: (1) establish whether the thresholds are likely to produce important regime shifts in the phosphorus cycle and eutrophication, and the conditions under which these regime shifts are likely to occur; (2) determine how key controlling variables such as climate, landscape characteristics, fertilizer applications, and management practices affect the thresholds; (3) evaluate the prospects for manipulating these control variables to mitigate eutrophication; and (4) assess changes in controlling variables that would increase

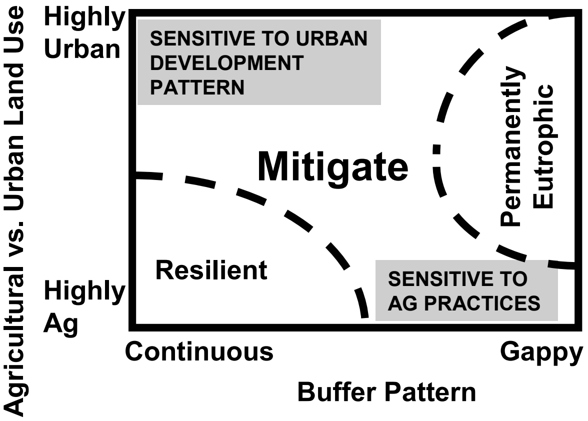

Figure 6. Hypothetical, simple example of model results. Dashed lines delimit regions of resilient and permanently eutrophic lakes from a region where mitigation is possible. Grey boxes indicate regions where risk of eutrophication is more sensitive to urban development practices or agricultural practices.

or decrease resilience of clear-water and eutrophic regimes. We will also produce a new integrated terrestrial-aquatic P dynamics model for the study of thresholds and resilience in watershed-lake systems that could be employed in other landscapes. Collectively, this work will create a comprehensive, data-driven, theoretically rich analysis of the spatial and temporal scales, controlling variables, and management implications of eutrophication thresholds and associated resilience in a complex, regional watershed-lake ecosystem.

Synthesis and Significance

Will ecosystem responses to human intervention will be smooth and continuous, discontinuous and unexpectedly large, or even catastrophic? This uncertainty is at the heart of many highly contentious environmental disagreements (Groffman et al. in review). Our proposed research will assess and characterize thresholds related to eutrophication, and thereby reduce uncertainty about the conditions for crossing ecological thresholds.

As a consequence of thresholds, ecosystem changes may be difficult or expensive to reverse. In many cases, the costs and delays of reversing eutrophication have come as a surprise to managers and a source of frustration to the public (National Research Council 1992). Our research will characterize thresholds for degradation and recovery in lakes subject to eutrophication, providing information that can reduce the incidence of surprise and support cost-effective planning for water-quality management.

If the costs of crossing thresholds are high, the preferred management strategy is to build resilience (Folke et al. 2002, Gunderson and Holling 2002). Lakes that are resilient to eutrophication could withstand brief perturbations of climate, land use, food web structure, or other factors without crossing thresholds to a eutrophic regime (Gunderson and Pritchard. 2002). Conversely, if a lake is in the eutrophic regime, then restoration involves crossing the threshold to a clear-water regime. In that case, resilience is a measure of the degree of intervention needed to restore the clear-water regime. That information is essential for evaluating the costs of mitigation, or comparing the costs and benefits of alternative approaches to mitigation. This project will analyze the aspects of resilience for watershed-lake ecosystems, providing a comprehensive assessment of the variables that control resilience of both clear-water and eutrophic regimes.

Regime shifts and their associated thresholds are likely to continue producing costly environmental surprises (Scheffer et al. 2001). Understanding and predicting thresholds associated with eutrophication of aquatic ecosystems could have numerous beneficial consequences for human livelihoods, health and well being in coming decades (Jones et al. 2000, Naiman and Turner 2000, Steffen 2004, Millennium Ecosystem Assessment in preparation for 2005 publication-b). This project will rigorously evaluate evidence for the existence and persistence of eutrophication thresholds, and explore practical approaches for working with them to achieve environmental goals. This project is an ideal opportunity because of decades of highly relevant data from the Yahara lakes, existing expertise in modeling, a strong legacy of eutrophication-related watershed-scale analyses, and strong public support for improved water quality in the region. Our research will contribute basic scientific knowledge of eutrophication thresholds: their spatial extent and location on the landscape; their biogeochemical characteristics; and the prospects for manipulating abiotic, biotic, and human factors that influence thresholds to mitigate eutrophication and increase the resilience of landscapes to lake eutrophication.

GENERAL PROJECT INFORMATION

Project Management

As co-PIs, Professors Steve Carpenter, Monica Turner and Jon Foley will jointly oversee the project and collaborate on all aspects of the research. To ensure rapid development of the integrated terrestrial-aquatic model, Foley will take primary responsibility for the climatic and hydrologic components, Turner will supervise the landscape ecology and terrestrial components of the model, and Carpenter will take primary responsibility for the lake model and the coordination of the overall terrestrial-aquatic model. This plan parallels our previous collaborative work on integrated terrestrial-aquatic models for the terrestrial-aquatic carbon cycle of lakes in Northern Wisconsin. Carpenter will oversee the statistical analyses of long-term limnological data.

This research also involves a collaborator from the Wisconsin Department of Natural Resources, Dr. Richard Lathrop, and a postdoctoral associate, Dr. Jeff Cardille. Lathrop and Carpenter will work together on the analyses of long-term limnological data. Cardille's primary responsibilities will involve development of the terrestrial-aquatic nutrient routing model in concert with the PIs.

The project will also benefit from other collaborations and activities. Dr. Motomi Genkai-Kato, a Japanese scientist who has collaborated with us in the past, is submitting a separate proposal to the Japanese Government to come to Madison to participate in this research. In addition, we will involve graduate students and postdocs from our ongoing Long-Term Ecological Research program and an affiliated Mellon Foundation program in the research.

Proposed Schedule

During Year 1, we will complete the statistical analyses of long-term limnological data. Steps of this process include (1) assembling the data sets through 2004 from existing data sources, (2) writing the programs for fitting the models and analyzing results, and (3) conducting the analysis, interpreting the results, and organizing results for publication. For the terrestrial-aquatic routing model, we will assemble the data layers and complete the programming, validation, and sensitivity analyses of the terrestrial component model. We expect to have papers ready for presentation at national meetings near the end of Year 1.

During Year 2, we will assemble the fully integrated terrestrial-aquatic P model, and conduct sensitivity analyses of it. We will run the numerical experiments needed to address our research questions, and develop synthetic graphics for communicating results. Papers from all components of the project will be prepared for submission and presentation at scientific meetings during Year 2, including the International Symposium "Regime shifts and recovery in aquatic ecosystems: challenges for management towards sustainability" co-organized by Carpenter.

Facilities and Equipment

This research will use the facilities of three units of UW-Madison: the Center for Limnology (Carpenter), Landscape Ecology Laboratory (Turner) and Center for Sustainability and the Global Environment (SAGE) (Foley). The three units are located within short walking distance on the UW-Madison campus, and are already engaged in several collaborations. Here we describe only the computing, modeling and statistical facilities germane to this project.

The **Center for Limnology** (http://limnology.wisc.edu) runs a 10/100 megabit local area network (LAN), with a 100 megabit connection to the campus wide area network (WAN). An 802.11b cloud supports wireless access throughout the Center. Three fileservers house a central repository of computer software and end-user data, and provide web services and administrative databases. One SUN Sparc Ultra 2 runs the LTER databases and web services. We maintain about 75 PC and Macintosh desktop and PC laptop computers, in addition to printers, slide shooters, slide and document scanners, fixed and portable computer projectors. We support standard office software, graphics software, and a variety of modeling, GIS and statistics software, as well as access to major electronic journals.

Facilities in the **Landscape Ecology Laboratory** (http://brahms.zoology.wisc.edu) will be used for most of the GIS and spatial analysis in this project. Networked computing facilities in Turner's laboratory include four Dell Xeon PC workstations, a Macintosh dual-processor G4, a Powerbook G4, a Sun Sparc 20 Unix workstation, a high-speed Hewlett Packard 600 dpi black-and-white printer, and a Tektronix Phaser 200i color printer. Software includes ArcGIS, ArcView, Matlab, S-Plus, R, SAS, Microsoft Office products, and the GRASS GIS package.

The **Center for Sustainability and the Global Environment** (SAGE) (http://www.sage.wisc.edu) has extensive computing facilities for the analysis of environmental data (including large remote sensing and GIS datasets) as well as for developing complex simulation models of the Earth's climate system, hydrological systems and biosphere. SAGE currently has a large network of Unix-based computing systems for supercomputing applications (a dedicated 18 processor -- and growing -- Unix / Mac OS X cluster with G5 processors, with 64 gigabytes RAM, and a 3 terabyte storage RAID disk system) as well as scientific applications (approximately 20 high-end Unix / Mac OS X workstations with G5 or G4 processors for computer model developing and data analysis, plus 4 high-end Pentium workstations running Windows XP for ArcGIS applications). SAGE also maintains a high-speed network (gigabit and 100-base T, plus wireless technology), plus a wide assortment of color and laser printers, computer projectors, etc. SAGE supports a dedicating computer classroom (with 12 Macintosh eMac systems running Unix / Mac OS X) and a portable laptop teaching system (with 12 iBook laptops).

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