

The primary objective of our study is to develop tools and understanding for complex systems of people and nature. Do socio-economic processes in conjunction with ecosystem responses lead to a complex system prone to surprise? Should nonlinear phenomena be invoked to explain or predict changes in these systems? We will address these central questions using a series of research approaches focused on lakes, their shoreline (riparian) systems, and the social and economic organizations of lake users.

Our concept of lake-riparian-social systems views the lake edge (shoreline and littoral zone) as a nexus of interaction. Human activity affects riparian forests and the density of fallen trees (coarse woody debris, CWD) in the lake. In some lakes humans introduce exotic species such as the rusty crayfish which can severely reduce densities of macrophytes in the littoral zone. Fish growth and community structure are tied closely to the refuges provided by CWD and macrophytes. Human attitudes and behaviors are in turn influenced by the appearance of the shoreline and the quality of fishing. Collectively, these feedbacks acting around the lake edge influence the organization of lake-riparian-social systems.

To understand the processes that create structure in lake-riparian-social systems, we propose to integrate new research from several disciplines (landscape ecology, limnology, mathematical economics, microbial ecology, paleoecology, population biology, resource economics, and theoretical ecology). Our approaches include theory development and interdisciplinary modeling; comparison of ecological and socio-economic variables across diverse systems; experimental manipulation of whole lake ecosystems and smaller field enclosures; and analysis of long-term and paleoecological data using new statistical tools from ecology and economics. Study sites are drawn from the hundreds of lakes within a one-hour drive of the University of Wisconsin Trout Lake Station near Boulder Junction, Wisconsin. Ecosystem manipulations will be conducted in partnership with the state management agency (Wisconsin Department of Natural Resources, WDNR).

This research will determine the extent to which nonlinear phenomena can explain and predict changes in lake-riparian-social systems. We will determine whether thresholds in riparian organization set the stage for collapse of fish production. We will also test the possibility that nonlinear dynamics can be used to design manipulations that extirpate invasive crayfish. If successful, this will cause a self-sustaining removal of an invading species – a path-breaking ecological restoration. Our general result will provide: (1) a template for basic understanding of biological complexity and (2) an example of success in the integration of socioeconomic and ecological systems.

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INTRODUCTION

The boundary of land and water appears so sharp that scientists once regarded lakes as microcosms (Forbes 1887). Human uses, institutions, and scientific studies of freshwater and land developed separately. Yet, there is increasing recognition that land and water are a critical nexus of interaction between people and nature (Naiman and DéCamps 1990, Holland et al. 1991, Covich 1993, Sparks 1995). Prominent aquatic ecologists recognize that freshwaters cannot be understood separately from surrounding lands (Hynes 1975, Likens 1984, Wetzel 1990), and land-water interaction occupies a central place in freshwater research agendas (Naiman et al. 1995). Policy analysts acknowledge that “Freshwater is emerging as one of the most critical natural resource issues facing humanity” (Hinrichsen et al. 1999), among the core topics of new international conventions addressing global environmental issues (Watson 1999). Yet we are just beginning to grasp the complex interactions of water, land, and people.

Despite ongoing scientific research, integrated ecological and socio-economic systems are difficult to understand and predict. Both ecological and social systems share many characteristics of complexity such as absence of a global controller, hierarchical organization, dispersed interaction, ongoing creation of novelty, selection and adaptation (Arthur et al. 1997, Holland 1995, Hartvigsen et al. 1998, Levin 1998, 1999, Milne 1998). Divergent outcomes can occur from similar points of origin, and small perturbations can evoke surprising reactions -- the hallmarks of biocomplexity. Models that incorporate nonlinearities and the possibility of complex dynamics may be necessary to understand the interactions of socio-economic and ecological systems.

Interactions of land, water and society in the Northern Highland Lake District of the Western Great Lakes region offer a superb system for bridging theory and practice in the study of complexity. This vast water-rich region includes thousands of lake + riparian systems across a heterogeneous landscape; strong interactions among components exhibiting a range of turnover rates (e.g. trees, people, fish, bacteria); and self-organized features (native or exotic species, ecological communities, ecosystem processes, anglers, lake user organizations). Gradual changes in land cover and land use correlate with a variety of abrupt changes such as fisheries collapses, species invasions, and conflicts among diverse groups of lake users.

Table 1. Dichotomies observed among lake-riparian-social systems of the Northern Highland Lake District of Northern Wisconsin.

Attribute	Dichotomy
Shoreline	wooded vs cleared
Nuisance Phytoplankton	absent vs variable
Woody Habitat	abundant vs sparse
Macrophytes	abundant vs sparse
Fish Growth Rate	high vs low
Large-bodied Piscivores	abundant vs rare
Piscivore Recruitment	frequent vs rare
Modes in Fish Size Distribution	no gaps vs gaps
Goal of Fishing	trophy vs food
Angler Organization	guides and clubs vs unstructured
Lake Shore Property Owners	organized vs not organized
Lakeshore Development	restricted vs unrestricted

System structures diverge into alternate states such as developed lakes vs. those protected as natural areas; lakes dominated by piscivorous vs. planktivorous fishes; or lakes dominated by low intensity, low impact recreation versus high intensity, high impact recreation uses. There are many features of lake-riparian-social systems that potentially span a continuum of states (Table 1). Despite this, very often only dichotomous extremes are observed. Can these dichotomies be understood

as linear trends driven by a hierarchy of exogenous factors? Or do concepts of bifurcation and multiple stability domains add explanatory power as we strive to understand and forecast land-water systems?

In our concept of integrated lake-riparian-social systems, physical structure in the shallow, nearshore (littoral) zones of lakes is the locus of key interactions. Physical structure consists largely of higher aquatic plants (macrophytes) and downed trees (coarse woody debris, or CWD) which are abundant in the littoral of most undeveloped lakes (Christensen et al. 1996, Swindale and Curtis 1957). This structure provides important foraging and reproductive habitat for many species of fishes and surface area for microbes and invertebrates, but is vulnerable to direct and indirect modification by lake-shore property owners and other lake users. Humans alter CWD amounts by direct removal from the lake or by clearing potential source trees from the riparian zone. Macrophyte densities can be reduced significantly by an exotic crayfish species, *Orconectes rusticus*, transported among lakes by humans. Human-induced reductions in physical structure can lead to altered recruitment and growth of fish with subsequent effects on other parts of the food web. These changes in lake quality, in turn, alter the perceived value of the lake to humans and lead to a variety of social, economic, and political responses. Lake, riparian and human processes self-organize through these mechanisms. We view littoral zone habitat as a master variable for understanding the transformations and reorganizations that create multiple structures of integrated lake-riparian- social systems.

PROPOSED RESEARCH

Overarching Questions: This proposal seeks explanations for the dichotomies observed among systems composed of lakes, riparian lands, and socio-economic components. We approach this problem by asking three questions. (1) Are the dichotomous structures of these systems best explained by processes that involve instability and divergent dynamics? (2) Should nonlinear phenomena be invoked to predict changes in these systems? (3) Do socio-economic processes in conjunction with ecosystem responses together lead to a complex system prone to surprises?

Proposal Organization: Our interdisciplinary research to address these overarching questions is organized in three clusters. Under **Theory and Modeling** we develop the conceptual and mathematical constructs necessary to understand limnological, riparian, and social systems. Under **Landscape Context**, we determine the diversity of lake-riparian-social systems, their spatial covariation on the landscape, and the suite of human and environmental drivers that are associated with various system states. We use **Whole-Lake Manipulations** to test for dichotomous states in lake-riparian-social systems predicted by models presented under Theory and Modeling.

Theory and Modeling

Theorists and field scientists will collaborate in developing models to explain the multiplicity of structures that arise in limnological, riparian and social systems. These models will then be tested using data to be collected by this project as well as a rich library of limnological time series from the North Temperate Lakes LTER and long-term experiments on lake acidification, eutrophication and food web manipulation. We plan both system-specific, detail-rich models

to make quantitative predictions about the lake-riparian-social systems, and broader models to draw general conclusions about the functioning of complex socioeconomic and ecological systems.

Theory of surprise for socioeconomic-ecological systems: In preliminary work, we have observed complex dynamics in models of institutions and boundedly-rational agents that interact to influence ecosystems (Carpenter et al. 1999). We will build upon such models to develop a theory of surprise for systems of people and nature. The common-sense explanation of surprise is simple. When agents make forecasts based upon observable variables, they inevitably omit dimensions of response by humans or ecosystems. Surprises occur when variables in these omitted dimensions either experience perturbations or are themselves influenced by management decisions. This sets up unexpected feedback loops between observed and unobserved variables. The notion of surprise can be formalized by borrowing on the large literature on the Le Chatelier principle. However, this literature does not consider the problems created by processes operating at different temporal and spatial scales. Our research will address this issue, and thereby explore a theory of surprise appropriate for the multiple scales that must be considered in ecological-social systems.

Multiplicity of socioeconomic structures: Are there thresholds of social organization that determine the spatial dynamics of anglers and the landscape pattern of lakefront property owners and lake property owner associations? Socioeconomic models will examine both complexity in the social system, such as the rapid movement of anglers among lakes and the effect of social systems on ecological systems. The analysis will focus in particular on heterogeneity of preferences among lake users and the implication of this heterogeneity for the dynamics of the social system. Some specific hypotheses are: (1) Factors affecting the response lag of anglers to a change in a fish population include the travel distance to the lake, the fish species in question, and the size of the angler population using the lake (which is related to the information available to anglers about fishing conditions); (2) Lake users on lakes without public access are more likely to organize associations; (3) The greater the economic value of a lake, the more likely are lake users to organize; (4) The greater the diversity of goods and services provided by the lake, the less likely are lake users to organize.

We will construct models addressing the individual behavior of anglers, lakefront property owners, and other lake users. These models will predict the response of lake users both to changes in relevant ecological factors (such as fish populations) and to changes in economic factors typically manipulated to direct human behavior, such as the cost of a fishing trip. For instance, models of lakefront property owners would cast the response to an ecological perturbation as the decision to (a) move to an alternative lake; (b) stay on the lake and take no mitigating action; or (c) stay on the lake and take actions to mitigate or reverse the perturbation. Fitting such models to data would require the methods advanced by Rust (1989, 1994) and others. Moreover, the nature of the decision process in this example emphasizes ambiguity in social feedbacks. For example, if lakefront property owners are avid anglers who respond to the reduction in fish populations by moving elsewhere, they might be replaced by owners with no interest in fishing who would clear the littoral zone of CWD. Thus, the initial decline in the fish population may lead to subsequent management decisions that further depress the fish population. If property owners instead choose to stay on the lake and take collective action to maintain the fish population, the social system may have a stabilizing effect on the ecological system.

Modeling of the dynamics of a social system rooted in many individual decisions will draw from two strands of literature. The first addresses social interaction models (e.g. Brock and Durlauf 1999), with special attention to spatial agglomeration (Arthur 1987 and Krugman 1996). The second is the literature beginning with Tiebout (1956) which examines whether people self-select into communities based on the value they place on various public goods. Self-selection of this sort will potentially stratify communities according to preferences for public goods, such as those produced by ecological systems (but see Stiglitz 1977, Brueckner 1982).

Spatiotemporal dynamics of riparian CWD input: How do land-use practices affect CWD input into lakes, and what types of practices most likely lead to such low CWD input that high fish populations cannot be sustained? The input of CWD into a lake will not only depend on the proportion of shoreline that is forested, but also on (a) the size-structure of the forest, since larger trees will produce more CWD, (b) the location of forested areas, since some locations (e.g., exposed peninsulas) will likely produce more CWD, and (c) the species composition of the forest, which may be particularly important as composition is influenced by forestry management and/or succession following large-scale natural disturbances. Summarizing the landscape surrounding a lake by a simple variable such as the proportion covered in forest will undoubtedly give poor estimates of CWD input into lakes. We will simulate forest dynamics and quantify the predicted input of CWD. The goal of this work is two-fold: first, it will demonstrate how surprises may arise when dimensions of a problem (e.g., forest size-structure) are not included in making predictions (see **Theory of surprise for socioeconomic-ecological systems**), and second, it will link forest structure and CWD production for historical studies (see **Landscape Context**) and models of fish dynamics (see **Thresholds for species invasion and collapse**).

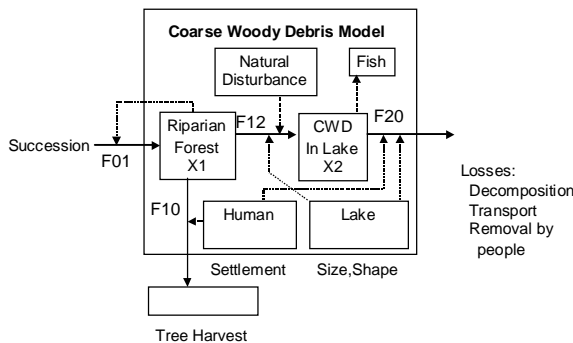


Fig. 1. Simulation model of CWD dynamics

A simulation model will be used to predict riparian CWD (density, basal area and structural complexity) through time at the level of an individual lake. The conceptual model (Fig. 1) illustrates the major state variables, flows and controls that will be quantified. Riparian forest development (**F01**) will be simulated by a

dynamic forest model (e.g., LANDIS, Mladenoff and He 1999) that accounts for successional dynamics and age-dependent changes in forest structure within 20 m of the lakeshore. CWD (**X2**) will be produced (**F12**) as trees die and

fall into the lake. Small frequent disturbances will produce gradual inputs of CWD, and stochastic catastrophic disturbances (e.g., Canham and Loucks 1984, Frelich and Lorimer 1991, Cardille et al. in press) will produce large pulses of CWD and reset the riparian forest to a pioneer stage. Human settlement will influence the abundance and structure of the riparian forest (**X1**) and loss of forest (**F10**) by (1) reducing the proportion of the lakeshore in riparian forest as clearing occurs for cottages and lawns, (2) reducing tree density and eliminating standing snags in the remaining forest, and (3) harvesting for timber. The state of CWD (**X2**) will be simulated by tracking its density, basal area, and structural complexity (e.g., log size and crown size and complexity). Losses of CWD (**F20**) will occur through: (1) decomposition, which is an extremely slow process influenced by species and log size; (2) physical transport

of logs to deeper portions of the lake by wind and water action; and (3) direct removal of CWD by people. Lake type (bog, seepage or drainage lake) and lake size will also influence transport of CWD and its removal by humans (both tend to be greater on larger lakes).

The model will be used to explore a variety of scenarios. Presettlement dynamics will be simulated for major riparian forest types (e.g., Mladenoff et al. 1993) and known probability distributions of natural disturbances (e.g., Canham and Loucks 1983, Frelich and Lorimer 1991). Effects of early settlement will be explored by simulating the extensive clearcutting that occurred during the late 1800s. Recent patterns of cottage development will be simulated based on observed rates of settlement around lakes of different type and size; alternative scenarios for future lakeshore settlement (varying rate, amount, and spatial location of development) will be compared.

Thresholds for Species Invasion and Collapse: Can changes in fisheries harvesting and the availability of refuge from predators destabilize lake ecosystems, leading to loss of species?

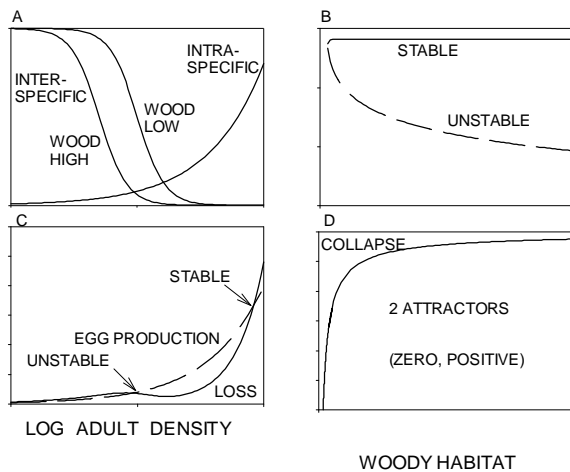


Fig. 2. Dependence of a piscivore driven by consumption of its juveniles by other species. A. Piscivore mortality rate from interspecific predation and intraspecific causes. Interspecific predation decreases as woody habitat increases. B. Stable and unstable densities of piscivore adults versus woody habitat. C. Egg production and total mortality of juvenile piscivores versus adult piscivore density, showing stable and unstable intersections. D. Bifurcation diagram for mortality rate of adults due to fishing and woody habitat, showing boundary between the zone of piscivore collapse and the zone where piscivores either persist stably or collapse, depending on initial conditions. Dynamics are generated by

$$A(t+1) = (1-k)A(t) + fA(t) (1 - mA(t) - p[A(t)])$$

where the function $p = \{ (1/w)^q / [(1/w)^q + A(t)^q] \}$.

A is adult piscivore density, k is mortality of adults due to fishing, f is fecundity, m is mortality due to intraspecific factors, and w is amount of woody habitat. Parameter values: f=0.3, m=0.008, and q=4.

Models to explore this possibility will incorporate angling harvest, refuges provided by CWD and macrophytes, impacts of invading crayfish on macrophytes, and size-structured predator-prey interactions. Here we present a pair of simple preliminary models that capture the essential known characteristics of fish and crayfish dynamics (Walters and Juanes 1993, Walters et al. 2000, Lodge et al. 1998, Olson et al. 1998, Schindler et al. 2000). We do not intend these models to be realistic portrayals of fish and crayfish dynamics, but instead use them heuristically to demonstrate the

plausibility and importance of alternative stable states.

Predator-prey interactions that change with growth of the participating species are an essential element of aquatic food webs (Ursin 1982). Size-structured interactions of juvenile piscivores, adult planktivores, and large-bodied adult piscivores have been shown experimentally to lead to a rich variety of relationships between predators and prey (Neill 1988, Persson 1988, Mittelbach and Osenberg 1993, Persson and Crowder 1998, Persson 1999). Refuges provided by macrophytes and CWD create an important arena in which size-structured interactions can occur.

A simple model illustrates divergent dynamics in a fish population dependent on CWD and exploited by anglers. Juveniles are subject to both density-dependent mortality and predation by other species (Fig. 2A). These other species are suppressed by high densities of piscivore adults. As CWD becomes more abundant, juvenile piscivores are sheltered from predation by other species. This leads to two equilibria, a stable one at high density of adult piscivores and a lower unstable threshold (Fig. 2B). If adult densities are perturbed below the threshold (e.g. by intense exploitation or a sequence of recruitment failures), the population collapses. The distance between the stable attractor and unstable threshold is increased by CWD (Fig. 2B). Thus, if CWD is abundant, the population can absorb a larger shock without collapsing. Fishing mortality and CWD interact to control the dynamic possibilities (Fig. 2D). If fishing mortality is too high or CWD is too low, stable persistence is not possible. Otherwise the population either persists at a high and stable level or collapses, depending on initial conditions and external shocks.

A similar model shows the possibility that invasive crayfish can be extirpated by harvesting large crayfish while increasing predation by fishes on small crayfish (Fig. 3). Fish predation on juvenile crayfish is inversely related to density of adult crayfish, which consume fish eggs and remove macrophytes essential for recruitment of fishes. At low harvest and predation rates, crayfish can invade and persist from a single gravid female. At intermediate levels of harvest and predation, two alternate states appear, with and without crayfish, separated by an unstable point. At high levels of crayfish harvest (or of fish predation, not shown), the positive attractor disappears and crayfish collapse.

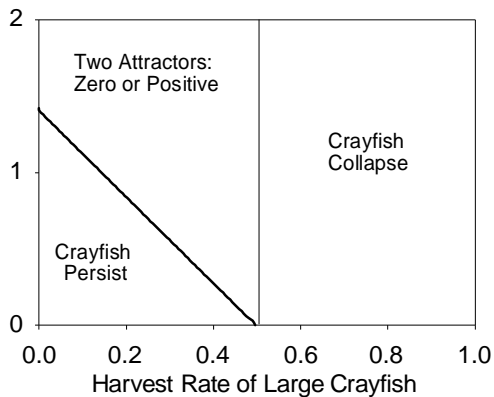


Fig. 3. Bifurcation diagram for model of crayfish population dynamics, showing different outcomes depending on harvest rate of large crayfish and predation by fishes on small crayfish. Dynamics were generated by $A(t+1) = (1 - k) A(t) + f A(t) \{1 - m A(t) - [c / (1 + A(t)^q)]\}$ where A is the adult crayfish population, k is mortality of adults from harvest, f is fecundity, m is density-dependent mortality, c is the predation coefficient for fishes consuming juvenile crayfish. Parameter values: $f=0.5$, $m=0.01$, $q=4$.

The potential existence of alternative stable states in both the fish and crayfish systems has important implications. In the fish model (Fig. 2), alternative stable states could cause a sudden loss of a fish population if, for example, a severe winter pushed fish densities below the threshold leading to extinction. In the crayfish model, the existence of alternative states would make it possible to eliminate crayfish by first reducing human fishing (thereby locating the system in the top left-hand corner of Fig. 3) and then engaging in an intensive harvesting program to push crayfish densities into the domain of attraction to the zero (extinct) state.

Statistical Detection of Nonlinearity: When do complexity-based approaches add value for understanding or predicting a system? Statisticians have developed diverse methods for detecting nonlinearities in ecological and economic data (e.g., Dennis and Taper, 1992; Turchin and Taylor 1992, Dennis et al. 1995, Ellner and Turchin 1995, Higgins et al. 1997, Kendall et al. 1999, Shintani 1999, Brock and Durlauf 2000). Our project features cross-

disciplinary exchange of these sophisticated and rapidly advancing methods. These will be applied to existing limnological time series (NTL-LTER, www.limnology.wisc.edu; Trophic Cascade Project, Carpenter and Kitchell 1993, Carpenter et al. 2000; Little Rock Lake experimental acidification, Frost et al. 1995, 1999) as well as paleoecological and comparative data collected in this study.

To evaluate potential for abrupt change, we will adapt nonparametric estimation techniques to test for presence of bifurcations in cases of slow moving dynamics forcing faster moving dynamics, as is common in ecosystems (Levin 1999). Shintani (1999) has recently extended work on kernel density estimation of stochastic dynamical systems of the form $X(t)=h[X(t-1),X(t-2),\dots,X(t-L)]+e(t)$ to estimate features of $h(\cdot)$ such as Lyapunov exponents. Since evidence of fully developed chaos is weak for our systems, we are more interested in features of $h(\cdot)$ associated with generators of abrupt change. Hence we plan to extend the work of Shintani and related work by Barnett, Brock, Dechert, Dennis, Ellner, Gallant, Gencay, Linton, Turchin and White to systems with variables having two or more distinctly different turnover rates, with an emphasis on detecting potential pathways to abrupt changes.

At the same time, we will take advantage of the multiplicity of connected lakes on the landscape to extend innovations in panel data analysis by Chamberlain, Heckman, Manski, Honore', Kyriazidou and others (review by Brock and Durlauf 2000). A key advance will be applications of these methods to test for thresholds in space or time hypothesized by our ecological and economic models, by extending the existing literature on computational Bayes' inference (Chamberlain and Imbens 1996, Geweke 1999, Amman et al. 1999).

Landscape Context

Our overarching questions, theories, and models focus on alternate states that may explain the dichotomous nature of lake-riparian-social systems. To understand the diversity of system structures and compare possible mechanisms for transitions among structures, we must confront models with data (Hilborn and Mangel 1998). Thus we will take advantage of the replicated lake-riparian-social systems to construct a comparative data set that will identify important lake, riparian, and social variables and processes. Our emphasis will be on collecting information across a gradient of lakes differing in abundance of littoral zone structure. These data will enable us to test our model predictions and address specific questions about temporal dynamics of CWD; patterns relating CWD, crayfish, macrophytes and fishes; microbial diversity; and associations of socio-economic and biophysical variables. Field studies addressing the following questions will be coordinated on a common set of lakes in the Northern Highland Lake District in northern Wisconsin (Frost et al. 1999).

Temporal dynamics of CWD: Is production of CWD a function of small, steady inputs (e.g., small, frequent disturbances) or is it dominated by occasional large pulses (e.g., large, infrequent disturbances)? What is the effect of shoreline development on the long-term dynamics of riparian forests and CWD? What are the time lags before reduced CWD inputs are detectable in the fish community?

Little is known about the long-term dynamics of production and accumulation of riparian CWD. A recent modeling study suggested that natural catastrophic disturbances (severe, large-scale events that result in replacement of the riparian forest) may bolster riparian CWD recruitment (Bragg 1997). Compared to dynamics in undisturbed old-growth forest, large natural

disturbances increased the temporal variability and net delivery of CWD, whereas clearcutting reduced both delivery and net amount for many years (Bragg 1997). Natural disturbance events in north temperate forests (e.g., extensive blow downs in northern Wisconsin in July 1976 and in the Boundary Waters Canoe Area in July 1999) produce large quantities of CWD that may persist in lakes for many centuries. We hypothesize that under presettlement disturbance regimes, CWD would have increased gradually in the lakes because inputs (both pulsed and gradual) would have exceeded rates of decomposition and loss to depth by physical transport. The CWD removal by humans associated with lakeshore development depletes the long-term resource of CWD while simultaneously reducing the source habitat. Christensen et al. (1997) found that CWD was inversely correlated with cabin density in 16 northern Wisconsin lakes. They estimated that it would take ~200 yr to replace the deficit in CWD density in densely settled lakes. Depending upon interactions between the slow and fast variables controlling the system, CWD may be pushed below the critical depensation level for fishes.

We will address these questions by studying the relationship between CWD and current and historic riparian land cover (see **Approach: Coordinated Field Studies**). These data will enable us to calibrate and test the long-term projections of the CWD model (described under **Theory and Modeling**).

Fish Relationship to CWD: What is the current correlation between CWD in lakes and their fish communities? Does the relationship between fish abundance (or growth rates) and CWD suggest the existence of alternative stable states?

Numerous studies demonstrate the potential importance of physical structure for fish dynamics (Crowder and Cooper 1982, Werner 1998, Persson and Crowder 1998). Refuges are often important for fish survival, and therefore play a large role in fish population dynamics (Walters and Juanes 1993, Walters and Korman 1999, Walters et al. 1999, 2000, Walters and Kitchell 2000). Pond experiments show that juvenile fishes seek refuge from predators by associating with macrophytes in littoral zones, and that refuge-seeking behavior has strong interactions with growth rate and fish body size (Mittelbach and Osenberg 1993, Jeppesen et al. 1998). Crayfish remove macrophytes and interact strongly with benthos and fishes (Lodge et al. 1998). Whole-lake experiments that opened channels in dense weedbeds increased fish growth rates (Olson et al. 1998). In contrast, fish growth rates were inversely correlated with CWD density in 13 northern Wisconsin lakes (Schindler et al. 2000). We plan a more complete analysis, especially considering the possible complications arising from alternative stable states, to investigate the association between physical structure and fish growth and abundance.

Data to address these questions (see **Approach: Coordinated Field Studies**) include estimates of CWD, as well as abundances, size- and age-distributions, and age-specific growth rates of fish species. If, in fact, alternative states in fish abundance occur at low CWD, then we would anticipate high variability in fish densities among lakes with low CWD, because lakes with low CWD could exist at either of the two alternative states (a given fish species present or absent). Even though patterns suggesting alternative stable states may not appear using fish abundance estimates (which are prone to high measurement error), the alternative states may be apparent in age-specific growth rates which can be measured more confidently (Carpenter et al. 1995).

Pelagic Ecosystem Processes and Microbial Diversity: Extreme differences in ecosystem drivers sometimes yield gradual or modest changes in ecosystem processes. This can result from shifts in species composition that stabilize process rates (Frost et al. 1993, Ives 1995a,b, Ives et al. 1999). If this compensation hypothesis is correct, we would expect substitutions of taxa with different responses to environmental drivers, leading to similar rates of ecosystem processes at different levels of the drivers (Ives et al. 1999). Microbial diversity and ecosystem respiration should be an excellent system to explore this hypothesis, because of rapid turnover rates and ease of experimentation. We predict that ecosystem respiration will show little variation among lakes, while microbial genomes show sharp differences and multiple configurations owing at least in part to differences in surface area associated with littoral zone structure. If this prediction is incorrect, we will determine the changes in microbial genetic diversity that are associated with trends in ecosystem respiration.

Socio-Economic Patterns: How do anglers, lakefront property owners, and lake associations create and respond to housing density, abundance of CWD and macrophytes, and fish populations?

Development of structural models of lake-user behavior will be accomplished using three types of data: (1) the response of anglers to perturbations such as CWD removal and loss of macrophytes due to crayfish invasion, as well as other cross-sectional data on angler behavior that relate to environmental goods and services (e.g., catch rates). These data will be used to estimate static or dynamic random utility models of angler behavior (e.g., Herriges and Kling 1999, Provencher and Bishop 1997). (2) Data on the formation and nature of private lake associations. (3) Data on the behavior of lakefront property owners and their tenants, and on the price and characteristics of lakefront property. These latter data will be used in hedonic analyses of the evolution of the price of lakefront property in response to changes in the goods and services provided by a lake (Palmquist 1994).

Approach: Coordinated Field Studies: The questions described above will be answered by field studies in a sample (N ~ 40) of lake-riparian-social systems. Study lakes will be stratified by landscape position (the relative hydrologic position of a lake within the local to regional flow system within a landscape, Kratz et al. 1997), housing density and forest type using existing data bases. These systems will be sampled for riparian, CWD, aquatic and social variables.

Riparian forest dynamics will be considered within 20 m of the lakeshore because most riparian CWD originates within this distance (Murphy and Koski 1989). The abundance of CWD (density, basal area, structural complexity, and state of decomposition) will be recorded along 50-m lengths of shoreline, and recent CWD will be distinguished from older CWD based on structural features (e.g., presence of bark, leaves and small branches.) The presence or absence of riparian forest will be mapped around each lake extending 20-m away from the lake. Forest structure (tree density and diameter-at-breast-height by species, stand age) will be measured in 10 randomly selected 100-m² plots (50-m length of shoreline x 20-m perpendicular to shoreline). Evidence of beaver activity and natural or anthropogenic disturbance will be noted in the field. Historical land use in the riparian zone will be obtained from aerial photographs and other historical records. The oldest aerial photos available for the region were taken in the 1930s

We will use paleoecological techniques to extend our time series of riparian vegetation, by analyzing cores from selected lakes for pollen and macrofossils of riparian trees and shrubs.

The relationship of near-shore sediment records to riparian vegetation composition will be calibrated using littoral surface sediment samples from lakes with contrasting nearby riparian vegetation (Davis et al. 1971, Bonny 1978, Sugita 1993, Calcote 1998). Transects of several (3-10, depending on slope) littoral sediment cores will be collected from target lakes and dated using ^{210}Pb and ^{14}C . Pollen, macrofossils, and sediment composition will be analyzed to reconstruct changes in lake level and riparian vegetation over time (a few hundred to ~2000 years).

Fish and crayfish communities will be sampled using an electroshocker, fyke nets, crayfish traps and beach seines using protocols developed by the NTL LTER project (<http://limnosun.limnology.wisc.edu/lppbite.html>) For each individual fish, species, length, and weight will be recorded and a scale will be taken for age determination. Macrophyte species composition and cover will be determined (Carpenter and Titus 1984).

Total ecosystem respiration will be measured by deploying automated buoys for continuous measurement of temperature, O_2 and pCO_2 in surface water (Carignan 1998, Cole et al. 2000). At the same time, microbial diversity will be determined by the same methods used by the Wisconsin Microbial Observatory program (Fisher and Triplett 1999, Delong et al. 1999, <http://www.limnology.wisc.edu/microbial/index.html>).

Surveys of anglers and lakeshore property owners will be used to obtain data on the behaviors and attitudes of these groups and determine their relationship to biophysical variables such as lake area, CWD, and fish abundance, as well as to social variables that affect the visual aspect of a lake, such as housing density. For behavioral models of property owners, survey data will be combined with other microeconomic data such as lakeshore housing prices and housing characteristics obtained from county government offices.

Whole-Lake Manipulations

Our models of CWD-fish and fish-crayfish-macrophyte interactions suggest instabilities that lead to divergent trajectories. Two issues are embedded in those results. First, is the instability due to ecological interactions? Second, does the combination of ecosystem and socio-economic components cause positive feedback? We can separate these issues by conducting large-scale ecosystem experiments. Because instabilities are transient, they are rarely observed, but they can be created experimentally. We will perform two whole-lake manipulations to test the hypothesis that population collapses involve unstable transitions. We will remove CWD from lakes, thereby creating compensatory responses in fishes. We will remove crayfish from a lake by intensive harvest combined by enhanced fish predation, which, in combination, create a new attractor leading to disappearance of crayfish (Fig. 3).

Whole-Lake Removal of CWD: Does gradual removal of CWD lead to recruitment failure of fishes and the eventual disappearance of some fish species from a lake? Or, does gradual removal of CWD lead to gradual changes in fish communities? We will answer these questions by removing CWD from two experimental lakes, while observing fish population dynamics in the experimental lakes and six lakes in which CWD has not been manipulated.

If the habitat removal leads to divergent changes in fish stocks, we expect to observe: (1) Recruitment failure in all piscivore stocks each year in the manipulated lakes, in contrast to occasional successful recruitment events by each piscivore species in the reference lakes over

the course of this grant cycle. (2) Size-specific growth rates of fishes in manipulated lakes will decrease as CWD removal decreases surface area for benthic production. No consistent changes in size-specific growth rate will occur in reference lakes. (3) Fish size structure will shift over time in the manipulated lakes. Specifically, limited refuge will expose juvenile fish to predation by larger fish, so recruitment to adulthood will only occur once the cohort of large adults has died off. This will produce gaps in the size structure. (Fig. 4). (4) Extirpation (local extinction) of fish species will occur in manipulated but not reference lakes. Extirpation may take longer than this 5-year grant cycle but will occur within the 10-year time horizon of the experiment. Note that in contrast to the simple heuristic models in **Theory and Modeling**, the data collected in this experiment contain fish size and age structure and transient dynamics. Thus, they contain far more information than simple estimates of total population size in unmanipulated systems. In conjunction with appropriate size- or age-structured models, these data can reveal a lot about the dynamics of the systems despite the relatively short duration of the experiments.

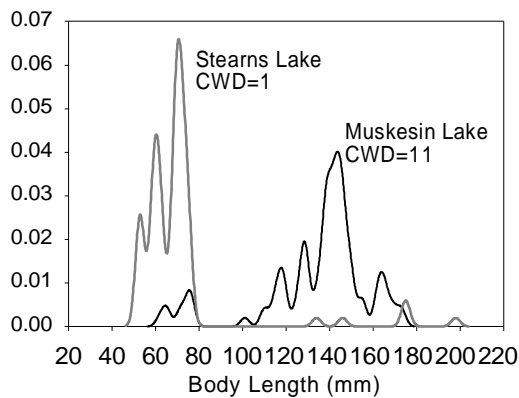


Fig. 4: Bluegill size distributions (fit to kernel density functions) for bluegill in Muskesin Lake (CWD = 11 per 50 m of shoreline) and Stearns Lake (CWD = 1 per 50 m of shoreline). Note broad gap in Stearns Lake between fish of length <80 mm and >130 mm.

Experimental plan: CWD will be removed from Nebish and Spruce lakes, while habitat will remain unmanipulated in Allequash, Big Muskellunge, Crystal, Escanaba, Sparkling and Trout lakes. All eight lakes lie within 15 km of Trout Lake Station. Escanaba, Nebish and Spruce lakes are part of the Wisconsin DNR's Experimental Lakes Area, and the other lakes are part of the North Temperate Lakes LTER site. Long-term pretreatment time series for fishes (18 to 44 years) are available for these lakes. Intensive pretreatment samples for fishes, benthos, and CWD will be collected from all eight lakes in early summer 2001. During summer 2001, CWD, defined as wood > 10 cm diameter at base, will be removed from the two manipulated lakes and stored onshore so it can be restored to the lakes

after the conclusion of the 10-year experiment in 2011. Throughout the experiment we will remove any trees that fall into the manipulated lakes. During summers of 2002-2005, fish species composition, populations, and size structures will be sampled by electroshocking, fyke netting, and beach seining. Scales will be taken for calculation of ages and growth rates. Stomach samples will be collected to determine diets. Samples of zooplankton and benthos will be collected to determine availability of invertebrate prey.

Anticipated results: This replicated ecosystem experiment will allow us to compare recruitment frequencies, size-specific growth rates, and shifts in size structure between manipulated and reference lakes using standard statistical methods. Size-specific growth rates are one of the most sensitive indicators of fish response to habitat manipulations, and our sample sizes will give adequate power to detect effects (Carpenter et al. 1995). Size distributions of species and functional groups will be compared using kernel-density estimators and bootstrap tests (Efron and Tibshirani 1993).

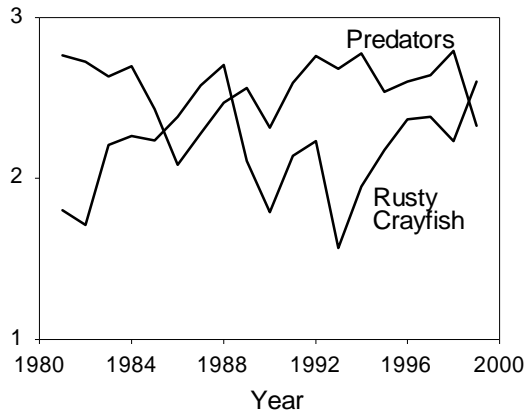


Fig. 5. Population density of rusty crayfish and predators (all fish individuals large enough to consume crayfish) in Sparkling Lake, 1981-1999.

Whole-Lake Removal of Exotic

Crayfish: The invading rusty crayfish, *Orconectes rusticus*, can have substantial effects on riparian habitat structure by drastically reducing macrophytes (Lodge et al. 1998) and we propose to alter these effects by experimental manipulations. These manipulations will be combined with our CWD experiments to evaluate complex responses to changing habitat structure. We will test the extent to which the rusty crayfish can be eliminated from a lake by intensive harvesting and increasing densities of its predators. Because crayfish invasions spread from a small

number of individuals, we expect that it will be impossible to eliminate rusty crayfish by trapping alone. However, crayfish are preyed upon by size selective predators such as largemouth and smallmouth bass, rock bass and walleye. Long-term data on crayfish and their predators suggest a strong reciprocal interaction (Fig. 5). In turn, crayfish predators are vulnerable to size selective predation by anglers. Harvest rates of these fishes are high in many of the lakes invaded by rusty crayfish. Unlike the native crayfish species, rusty crayfish can become so large that they are not vulnerable to fish predators. Large crayfish eliminate macrophyte beds which serve as fish habitat especially for the young of year and juveniles. This is the series of cause and effect often seen in lakes when diverse fish and macrophyte communities shift to a condition of bare substrates, few fishes and extremely abundant crayfish. We hypothesize that rusty crayfish can be eliminated by intensive trapping of adults combined with increased mortality on the young crayfish resulting from enhanced populations of fishes that consume smaller crayfish. In biocomplexity terms, with high fishing mortality there is one attractor characterized by high crayfish, low fish habitat (in this case macrophytes), and low fish stocks (see **Theory and Modeling**). With reduced fishing and heavy trapping of crayfish, we create a threshold for crayfish collapse.

We will test this hypothesis by trapping crayfish intensively in Sparkling Lake with newly designed, large-scale crayfish removal gear. At the same time, we will collaborate with the Wisconsin DNR to establish and maintain fishery management practices that will increase the abundance and average individual size for largemouth bass, smallmouth bass, rockbass, and walleye populations. These will include stocking of largemouth, smallmouth and walleye, increased size limits, decreased bag limits, and a catch-release public awareness campaign. If the hypothesis is correct, we will eliminate the invading crayfish from the lake, macrophyte abundance and diversity will increase, and rates of fish growth and survival will increase.

Experimental Plan: The necessary pretreatment data (> 18 years) exist. In spring 2001, we will initiate intensive removal of crayfish while increasing abundance of walleyes and smallmouth bass and reducing harvest of all fish that prey on crayfish. Variables measured in Sparkling Lake and the reference lakes (Allequash, Big Muskellunge, Crystal, and Trout, all part of NTL-LTER) will include fish community composition, size structure, diets and growth rates; crayfish abundance; and macrophyte abundance. As internal controls, we will establish replicate crayfish exclosures (100 m²) in Sparkling Lake and in several reference lakes in

which macrophytes and benthos will be measured. Exclosures will be compared to replicate areas of the same size that are open to crayfish still present in the treatment and reference lakes. Crayfish densities will be measured continuously through the removal period by depletion (DeLury) estimates (Hilborn and Walters 1992). Macrophyte recovery in exclosures versus areas open to crayfish will be analyzed by repeated-measures ANOVA.

Anticipated results: Disappearance of crayfish can only be explained by a model in which a threshold has been crossed so that zero is an attractor for crayfish density. This could result from enhanced densities of predators. Simply demonstrating the elimination of crayfish will implicate fish predation as an important component of the system, because in the presence of angler pressure, the zero boundary of crayfish abundance is known to be unstable (since crayfish initially invaded from low density). Further evidence for alternative stable states will appear as an accelerating decline in crayfish abundance once it crosses into the domain of attraction to the zero state.

Synthesis and Significance

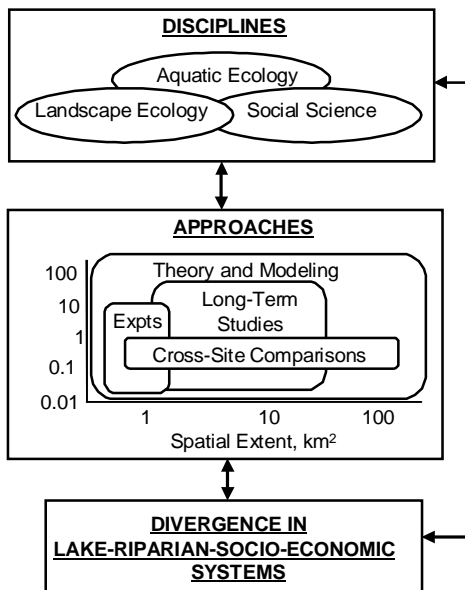


Fig 6. Disciplines and approaches used to understand and predict divergence of lake-riparian-social systems.

The search for explanatory and predictive power begins with recognition of distinctions among contrasting states of a system. Integration that embraces contrast leads to understanding (Pickett et al. 1995). Insights that prompt integration often arise from multiple perspectives on the same phenomena. We recognize contrast among lake-riparian-social systems, and seek explanations and predictions in appropriate disciplines and complementary approaches (Fig. 6).

Understanding lakes in a human-dominated landscape is not a problem in aquatic ecology, or landscape ecology, or social science. It is a problem in all these disciplines jointly. An integrative theory must account for the structural diversity of socio-economic systems as well as multiple spatial and temporal scales in ecology. Riparian vegetation has a slow turnover rate compared to those of fish populations or markets for recreational opportunities. Woody habitat takes centuries to degrade; thus a fallen tree structures ecosystem processes for many generations of

aquatic organisms. Macrophytes, in contrast, can change rapidly with invasion of crayfish. Both macrophytes and fallen trees vastly increase the surface area for primary production, microbial metabolism, and invertebrate production while providing essential habitat for fishes. People make decisions while learning about environments they co-create, and thereby self-organize diverse socio-ecological systems that have profound ecological consequences. We will model and measure these complex interactions, and determine whether and how they create systems prone to surprise.

Understanding of systems of people and nature will not derive from theory, comparison, experiment, or long-term data alone; it will emerge from all of these approaches together (Pace and Groffman 1999). These approaches, used in all disciplines, are complementary. Theory offers enormous flexibility in space and time, general insight and predictive power, but theory must be grounded in observation. Observations, though essential, are scale- and method-dependent. Comparisons of diverse lake-riparian-social systems reveal the diversity of system structures and spatial patterns that a comprehensive theory must explain. Long-term data expose temporal variability and instabilities to be explained by theory. Both comparative and long-term results, however, may be ambiguous with regard to mechanisms. Experiments, while bound to particular scales, allow tests of mechanism and comparison of alternative models for system transformation. Triangulation among all three observational approaches is needed to guide the evolution of theory and the development of management practices. We will coordinate all of these approaches to test fundamental ideas about the complexity (or simplicity) of lake-riparian-social systems.

Our research will show whether and how nonlinear phenomena can explain changes in lake-riparian-social systems. These insights will illuminate the more general issue of making forecasts for use by decision makers of potentially divergent systems (Chichilnisky 1999, Heal 1998). The prediction problem for systems subject to divergent dynamics is a generic one in environmental management, arising for example in global climate change (Rahmstorf 1997, Taylor 1999), nonpoint pollution (Carpenter et al. 1999) and fisheries (Walters 1986, Lierman and Hilborn 1997). Riparian management is among the most contentious issues in Wisconsin and other regions where water resources are central to environmental policy. A key question, to be resolved by this study, is whether thresholds in riparian land cover set the stage for collapse of fish stocks. We will also determine whether an invasive species can be extirpated by taking advantage of a nonlinearity in its connections to the food web. If successful, this will be a rarity in ecological restoration - self-sustaining removal of an invasive species. This innovation could be crucial for restoration of freshwater systems, which harbor 47% of the endangered species in the United States (Jackson et al. 2000) and are especially susceptible to species invasion (Sala et al. 2000).

Data Dissemination

We will emphasize rapid distribution of data and models to facilitate theses, models and publications driven by specific hypotheses in the proposal. Data acquisition occurs during the summer field season. Before the end of December each year, data from that year's field season will be available for analysis, writing, and planning. Data and metadata will be made available as flat text files for ease of assimilation by diverse software. To supplement the metadata, we will develop a project-wide methods manual and place it on our web site. We will also publish data, metadata, and models on the web site. Data will be made available publicly within two years of collection.

Research Timetable

Because of the integrated nature of the modeling, theory development, field observations and manipulations proposed here, all phases will occur simultaneously. Theory development, modeling, and analysis of existing time series will begin immediately. Field observations and whole-system manipulations will start in summer 2001 and continue until the end of the project. Theory development and modeling will occur concurrently with the field program. Although we

have planned the whole-lake manipulations to run through 2011, we expect to see significant manipulation effects in this grant cycle.

Results of Prior NSF Support

Comparative Study of a Suite of Lakes in Wisconsin -- North Temperate Lakes Long-Term Ecological Research (NTL-LTER). Steve Carpenter and 18 co-PIs. DEB 96-32853. October 15, 1996 - October 15, 2002. \$6M.

This Biocomplexity proposal emphasizes theory, comparison and experimentation. It builds on a strong foundation of long-term observation established by the North Temperate Lakes Long-Term Ecological Research program (NTL-LTER) started in 1981. The goals of the NTL-LTER program are to detect long-term change in lakes and surrounding landscapes; understand physical, chemical, and biological linkages at lake, landscape, and regional scales; and understand feedbacks between lakes and human processes. Seven lakes in northern Wisconsin and four lakes in southern Wisconsin serve as foci for this work. Since 1997, the project has produced more than 125 peer-reviewed publications and 14 graduate student theses. Descriptions of the NTL-LTER program, publication lists, and core data sets are available at the NTL web page <<http://limnosun.limnology.wisc.edu>>

The work we propose is distinct from the NTL-LTER project. The comparative landscape studies and the whole-lake CWD removal involve lakes that are not part of the LTER program. NTL-LTER does not have sufficient resources or the appropriate collection of investigators to conduct the research package in this proposal. Consequently, five co-Principal Investigators on this proposal are not affiliated with the LTER program: Brock, Hotchkiss, Ives, Kitchell and Provencher. The distinctive questions and approaches of this proposal complement those of the NTL-LTER project. Clearly the proposed work will benefit from the understanding of the Northern Highland Lake District developed from nearly 2 decades of LTER research. In addition, it will make unique contributions to our understanding of biocomplexity in lake-riparian-social systems.

Project Organization

All project personnel are affiliated with the Madison campus of the University of Wisconsin. Co-location will simplify coordination, making it relatively easy to organize meetings or contact other project personnel as the need arises. Many of the PIs already collaborate.

Twice each year we will hold a 2.5 day meeting gathering all project faculty, staff and students in one place to review data, work together on publications, and plan. One meeting will occur at Trout Lake Station each May, just after classes end, to launch the field season. The other meeting will occur in Madison each January, just before classes start, to review data, organize analyses, modeling, and writing tasks for the spring semester, and plan. In addition to these regular semi-annual meetings, the PIs will meet at least once per semester to review budget, make policy decisions, and discuss progress.

Responsibilities for the major program elements will be divided among the PIs as follows. The Project Director is Carpenter and the Field Coordinator is Kratz. Theorists are Allen, Brock and Ives; in addition, Carpenter and Turner will make significant contributions to modeling. Integration of theory and field work is a major goal of the project. Thus the theorists will not be insulated, but instead will work closely with the various data-driven components of the project. All PIs will participate in statistical analyses, though for leadership we will turn to Brock, Carpenter, Ives and Turner who have substantial experience in the various time-series methods, spatial statistics, panel analysis, nonparametric Bayes', and scaling law approaches that will be used to interpret our results. These PIs will participate in the analysis of existing long-term data along with the scientists most familiar with those data sets: Benson, Frost, Kratz and Magnuson. The comparative study of diverse lakes involves riparian ecology, socio- economics, limnology, microbiology and paleoecology. PIs responsible for organizing the field work are Frost, Hotchkiss, Kitchell, Kratz, Provencher, Triplett, and Turner. The whole-lake manipulation of CWD centers on responses of fishes, benthos, and plankton. PIs responsible for organizing the field work are Carpenter, Frost, Kitchell, and Kratz. The whole-lake manipulation of crayfish centers on responses of the crayfish themselves, macrophytes and benthos. PIs responsible for organizing the field work are Frost, Ives, Kratz and Magnuson.

Data entry, QA/QC, and preparation of metadata will be carried out by the field team leaders under the supervision of Kratz. Benson will supervise other aspects of information management, including organization of data sets and posting of data, metadata, and the methods manual on the Internet.

Educational Activities

Outreach, education and training activities will reach multiple constituencies, including local citizen groups, other scientists, postdocs, graduate students, undergraduates, and K-12 students. Our ecosystem experiments will require significant public education and outreach. While the WDNR has lead responsibility for informing the public of these experiments, UW scientists will contribute many presentations to the public meetings. In previous large-scale experiments on public lakes, we have found the goodwill generated by such presentations to be valuable in many ways beyond the success of the experiment itself.

Graduate education will be closely integrated with all aspects of this research, and represents the most intensive educational effort of the project. We have budgeted for six graduate students. However, these funds will be leveraged substantially through Fellowships and Teaching Assistantships (most Ph.D. programs require that students teach for at least a year). Based on experience with similar interdisciplinary programs, we expect that the six student positions will support a total of 10 to 12 graduate students working on the project.

Whenever appropriate, we will arrange co-supervised interdisciplinary Ph.D. programs for students affiliated with this project. In our experience, it “takes a whole village” of diverse senior scientists to train a graduate student. The most exciting ideas of this project lie at disciplinary interfaces, such as theory - practice, ecology - economics, riparian – paleo ecology, riparian - fish ecology, socio-economics – food web ecology and others. Flexible graduate programs at UW-Madison facilitate innovative training tailored to interdisciplinary opportunity.

While student projects and supervisory arrangements will be negotiated as students are recruited, a number of excellent thesis areas are already identified. Some examples:

- Sources, sinks and spatial heterogeneity of woody habitat in lakes: evidence for thresholds?
- How did the deforestation event of 1900 change north temperate lakes?
- Relationship of ecosystem respiration to microbial genetic diversity in lake ecosystems
- Detection, mechanisms, and implications of critical depensation in littoral fishes – the role of woody habitat
- Manipulation of thresholds to extirpate invading crayfish – theory and practicality
- Mechanisms and divergence in self-organization of lake users – implications for incentives and regulation
- The temporal-spatial dynamics of unregulated lakeshore development, and its implications for the management of complex lake ecosystems
- Uncertain thresholds in resource management: implications for decision analysis
- Alternative stable states and the rate of invasion of an exotic crayfish

- Transient dynamics of size-structured populations: theory and data from a whole-lake manipulation
- Paleological reconstruction of the riparian habitat of north temperate lakes: comparing natural and human disturbance characteristics

Communication of results will be accelerated by a workshop on Complexity in Ecological-Social Systems, to which a diverse cross-section of relevant scientists will be invited. This workshop will publicize our discoveries and give the opportunity for us to learn from others. The workshop will be held at Trout Lake Station, near the end of year 3 or beginning of year 4. At this time in the project, synthesis will be accelerating and broad discussion is likely to reveal novel opportunities.

Both graduate and undergraduate courses will be enhanced by material to be developed in this project. Most of the PIs have substantial teaching roles in UW, and some of us are responsible for large undergraduate courses where insights from this project will reach a large number of students. Examples of large courses taught by the PIs include Introductory Biology, Introductory Ecology, General Ecology, Limnology, Conservation of Aquatic Resources, and Environmental Economics. Also, insights and methods from the project will directly enhance many smaller courses for graduate students and upperclass undergraduates taught by the PIs.

Direct enhancement of undergraduate training will occur in several ways. We have budgeted for undergraduate field assistants. These students will develop independent study or honors thesis projects based on data that they help collect through their participation in field programs. In addition, UW has a number of summer research fellowships available for undergraduates, some of them managed through the endowment of the Center for Limnology and the Department of Zoology. The competition for these funds attracts the best and brightest undergraduates, and we plan to offer them exciting opportunities through this project. Finally, we will be aggressive in pursuing any supplementary undergraduate funding offered by NSF, such as REU funds.

At the K-12 level, project results will be incorporated into our existing Schoolyard LTER project. We have partnered with local elementary schools and offer them teacher training, access to professional scientists, and field experience for K-12 students. Several hundred elementary students participate directly each year in this program.

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BIOGRAPHICAL SKETCH

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Appointments: Assistant Professor to Associate Professor, Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 1979-1989; Associate Professor to Professor, Center for Limnology and Department of Zoology, University of Wisconsin, Madison, Wisconsin 1989-present.

Synergistic Activities (selected): President-Elect, Ecological Society of America, August 1999; Co-Editor in Chief, *Ecosystems*; Editorial Boards of *Conservation Ecology and Issues in Ecology*; Chair, Science Advisory Board, Resilience Alliance.

Selected Honors: Pew Fellow in Conservation and Environment; Per Brinck Award in Limnology (Lund University); G. E. Hutchinson Medal (American Society of Limnology and Oceanography); Kellett Mid-Career Award (U. Wisconsin-Madison Graduate School)

Five Publications Closely Related to This Proposal (from >165 research papers and 2 books since 1976)

Carpenter, S.R., K.L. Cottingham, and C.A. Stow. 1994. Fitting predator-prey models to time series with observation errors. *Ecology* 75: 1254-1264.

Carpenter, S.R., S.W. Chisholm, C.J. Krebs, D.W. Schindler and R.F. Wright. 1995. Ecosystem experiments. *Science* 269: 324-327.

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Five Additional Publications

Carpenter, S.R. (ed.). 1988. *Complex Interactions in Lake Communities*. Springer-Verlag, NY.

BIOGRAPHICAL SKETCH

(This is a continuation page)

Carpenter, S.R. and J.F. Kitchell (eds.). 1993. *The Trophic Cascade in Lakes*. Cambridge University Press, London.

Carpenter, S.R., P. Cunningham, S. Gafny, A. Munoz del Rio, N. Nibbelink, M. Olson, T. Pellett, C. Storlie and A. Trebitz. 1995. Responses of bluegill to habitat manipulations: power to detect effects. *North American Journal of Fisheries Management* 15: 519-527.

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Research published during the last two years (My Proposal builds on these).

Brock, W., Hommes, C., (1997a), "A Rational Route to Randomness," *ECONOMETRICA*, Volume 65, No. 5, pp. 1059-1095.

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Brock, W., (1999), "Whither Nonlinear?", *JOURNAL OF ECONOMIC DYNAMICS AND CONTROL* (in press).

Brock, W., de Fontnouvelle, P., (1999), "Expectational Diversity in Monetary Economics," *JOURNAL OF ECONOMIC DYNAMICS AND CONTROL* (in press).

Brock, W., Durlauf, S., (1999), "A Formal Model of Theory Choice in Science," *ECONOMIC THEORY* (in press).

Brock, W., Durlauf, S., (1999), "Interactions-Based Models," prepared for Leamer, E., Heckman, J., eds., *HANDBOOK OF ECONOMETRICS: V*, North Holland: Amsterdam.

Brock, W., (1999a), "Scaling in Economics: A Reader's Guide," *INDUSTRIAL AND CORPORATE CHANGE* (in press).

Brock, W., (1999b), "Whither Nonlinear?", *JOURNAL OF ECONOMIC DYNAMICS AND CONTROL* (in press).

Carpenter, S., Ludwig, D., Brock, W., (1999), "Management of Eutrophication for Lakes Subject to Potentially Irreversible Change," *ECOLOGICAL APPLICATIONS* (in press).

Carpenter, S., Brock, W., Hanson, P., (1999), "Ecological and Social Dynamics

in Simple Models of Ecosystem Management," CONSERVATION ECOLOGY, 3 (2) online
<http://www.consecol.org/journal/vol3/iss2/art4>.

Some Relevant Publications not listed in the References

3. Brock, W., (1972), "On Models of Expectations that Arise from Maximizing Behavior of Economic Agents over Time," JOURNAL OF ECONOMIC THEORY, December, 348-376.

4. Brock, W., (1993), "Pathways to Randomness in the Economy: Emergent Nonlinearity and Chaos in Economics and Finance," ESTUDIOS ECONOMICOS, Vol. 8, # 1, January-June, pp. 3-55.

5. Brock, W., Lakonishok, J., LeBaron, B., (1992), "Simple Technical Trading Rules and the Stochastic Properties of Stock Returns," JOURNAL OF FINANCE, 47, (5): 1731-1764.

6. Brock, W., Hsieh, D., LeBaron, B., (1991), NONLINEAR DYNAMICS, CHAOS, AND INSTABILITY: STATISTICAL THEORY AND ECONOMIC EVIDENCE.

Website: <http://www.ssc.wisc.edu/~wbrock>.

My website contains CV, a complete list of papers as well as working papers, and a brief "activities report" which reviews contents of many of my recent papers. My joint work with Hommes played a role in enabling him to win a Dutch competition to fund a recent Center in Amsterdam called Center for NonLinear Dynamics in Economics and Finance (<http://www.fee.uva.nl/cendef>), "CeNDEF" for short. See the center's website for details.

Working papers relevant to this proposal are:

Brock, W., Starrett, D., (1999), "Nonconvexities in Ecological Management Problems," (J. ENV. ECON. AND MANAGEMENT, submitted)

Brock, W., Xepapadeas, A., (1998), "Optimal Ecosystem Management when Species Compete for Limiting Resources," (J. ENV. ECON. AND MANAGEMENT, revised version under review).

Dechert, W., Brock, W., (1999), "Lake Game."

References to this proposal shall include the above papers plus a reference list that does not include these.

COLLABORATORS (previous 4 years): Steven Durlauf, Department of Economics, University of Wisconsin; Cars Hommes, Department of Economics, University of Amsterdam, The Netherlands; Blake LeBaron, Department of Economics, Brandeis University; Patrick deFontnouvelle, Economics Group, SEC, Washington, D.C.; Steve Carpenter and P. Hanson, Department of Limnology, University of Wisconsin; Donald Ludwig, Department of Zoology, University of British Columbia; David Starrett, Department of Economics, Stanford University; W. D. Dechert, Department of Economics, University of Houston; Marten Scheffer and Milena Holmgren, Aquatic Ecology and Water Quality Management Group and Forest Ecology, Wageningen Agricultural University, Wageningen, The Netherlands; Tasos Xepapadeas, Department of Economics, University of Crete, Crete, Greece; Frances Westley, Faculty of Management, McGill University, Montreal, Canada. UW graduate student Kim-Sau Chung (placed at Northwestern) has been supported by my NSF and UW graduate student Artur Minkin is currently being supported.

BIOGRAPHICAL SKETCH

Anthony R. Ives - Biographical Sketch

Address: Department of Zoology, University of Wisconsin-Madison, Madison, WI 53706. Tel. 608-262-1519.

arives@facstaff.wisc.edu

Professional Preparation: B.A. in Biology and B.A. in Mathematics, Valedictorian, University of Rochester, 1983; Ph.D. in Biology, Princeton University, 1988.

Appointments: Life Sciences Research Foundation Postdoctoral Fellowship, University of Washington, 1988-1990; Assistant Professor, Zoology, UW-Madison; 1990-1996; Associate Professor, Zoology, UW-Madison, 1998-.

Selected Honors: Romnes Fellowship (early career development), UW-Madison Graduate School, 2000-2005; Vilas Fellowship, UW-Madison Graduate School, 1999-2000; Lilly Foundation Teaching Fellowship, UW-Madison, 1994; Charlotte E. Proctor Honorable Fellowship for Outstanding Graduate Research, Princeton University, 1988.

Five Publications Closely Related to This Proposal (from >50 research papers since 1985)

Ives, A. R. 1995. Predicting the response of populations to environmental change.

Ecology 76: 926-941.

Ives, A. R. 1995. Measuring resilience in stochastic systems. *Ecological Monographs* 65: 217-233.

Ives, A. R., and V. A. A. Jansen. 1998. Complex dynamics in stochastic tritrophic models. *Ecology* 79: 1039-1052.

Ives, A. R., S. R. Carpenter, and B. Dennis. 1999. Community interaction webs and the response of a zooplankton community to experimental manipulations of planktivory. *Ecology* 80: 1405-1421.

Ives, A. R., K. Gross, and J. L. Klug. 1999. Stability and variability in competitive communities. *Science* 286: 542-544.

Five Additional Publications

Ives, A. R. 1996. Evolution of insect resistance to *Bacillus thuringiensis*-transformed plants. *Science* 273: 1412-1413.

Losey, J. E., A. R. Ives, J. Harmon, C. Brown, and F. Ballantyne. 1997. A polymorphism maintained by opposite patterns of parasitism and predation. *Nature* 388: 269-272.

Ives, A. R., and W. H. Settle. 1997. Metapopulation dynamics and pest control in agricultural systems. *American Naturalist* 149: 220-246.

Ives, A. R., S. S. Schooler, V. J. Jagar, S. E. Knuteson, M. Grbic, and W. H. Settle. 1999. Variability and parasitoid foraging efficiency: a case study of pea aphids and *Aphidius ervi*. *American Naturalist* 154: 652-673.

BIOGRAPHICAL SKETCH

(This is a continuation page)

Klug, J. L., J. M. Fischer, A. R. Ives, and B. Dennis. 2000. Compensatory dynamics in planktonic community responses to pH perturbations. Ecology 81: 387-398.

Collaborators in Past 48 Months (In addition to advisees and Co-PIs of this proposal):

J. H. Brown, R. French-Constant, K. L. Cottingham, B. Dennis, J. M. Fischer, M. Grbic, M. E. Hochberg, V. A. A. Jansen, J. L. Lawton, D. L. Murray, W. H. Settle, S. S. Schooler, M. Taper, D. Tilman

Graduate and Post-graduate Advisors: Bob May, Peter Kareiva

Advisees (graduate and postdoctoral): Ed Emmons, Johannes Foufopoulos, Kevin Gross, Eric Klopfer, Jen Klug, John Losey, Todd Palmer, Nancy Schellhorn, William Snyder

BIOGRAPHICAL SKETCH

Timothy K. Kratz (Center for Limnology, University of Wisconsin Trout Lake Station)

Born: 1 September 1952;

Education:

B.S. Botany, University of Wisconsin-Madison, 1975

M.S., Ecology and Behavioral Biology, University of Minnesota-Twin Cities, 1977

Ph.D., Botany, University of Wisconsin-Madison, 1981.

Employment:

1997-present: Senior Scientist, Center for Limnology, University of Wisconsin-Madison

1997-1999: Acting Associate Director for the Trout Lake Station

1988-1997: Associate Scientist, Center for Limnology, University of Wisconsin-Madison

1985-1988: Assistant Scientist, Center for Limnology, University of Wisconsin-Madison

1981-present: Site Manager, North Temperate Lakes LTER Project

Professional Activities:

NAS National Research Council Committee on the Grand Canyon Monitoring and Research Center, 1998-1999

LTER Network Executive Committee, 1997-present

NSF Ecosystems Studies Review Panel, 1997-present

NSF/EPA Decision Making and Valuation Review Panel, 1996

NSF TECO Review Panel, 1995

NAS National Research Council Committee on Environmental Monitoring and Assessment Project, 1991-1995

Editor, Newsletter of the Association of Ecosystem Research Centers, 1988-1993

Member: ESA, ASLO, SIL

Five Publications Closely Related to This Proposal

Bolgrien, D. W., and T. K. Kratz. 2000. Lake shore riparian areas. Pages 207-217 in Verry, E. S., J. W. Hornbeck, and C. A. Dolloff (eds.) Riparian Management in Forests of the Continental Eastern United States. Lewis Publishers, Washington D.C.

Gergel, S. E., M. G. Turner, and T. K. Kratz. 1999. Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers. Ecological Applications 9(4):1377-90.

Kratz, T. K., B. J. Benson, E. Blood, G. L. Cunningham, and R. A. Dahlgren. 1991. The influence of landscape position on temporal variability in four North American ecosystems. American Naturalist 138:355-378.

Kratz, T.K., P.A. Soranno, S.B. Baines, B.J. Benson, J.J. Magnuson, T.M. Frost, and R.C. Lathrop. 1998. Interannual synchronous dynamics in north temperate lakes in Wisconsin, USA. Pages 273-287 In George, D.G., J. G. Jones, P. Puncochar, C. S. Reynolds, and D. W. Sutcliffe (eds.) Management of Lakes and Reservoirs during Global Climate Change. Kluwer Academic.

Kratz, T. K., and T. M. Frost. 2000. The ecological organization of lake districts: general introduction. Freshwater Biology. (in press).

BIOGRAPHICAL SKETCH

(This is a continuation page)

Five Additional Publications

Cole, J. J., N. F. Caraco, G. W. Kling, and T. K. Kratz. 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* 265:1568-1570.

Baines, S. B., K. E. Webster, T. K. Kratz, S. R. Carpenter, and J. J. Magnuson. 2000. Synchronous behavior of temperature, calcium and chlorophyll in lakes of northern Wisconsin. *Ecology*. (in press).

Kratz, T. K., T. M. Frost, J. E. Elias, and R. B. Cook. 1991. Reconstruction of a regional, 12000-year silica decline in lakes by means of fossil sponge spicules. *Limnology and Oceanography* 36:1244-1249.

Kratz, Timothy K., Barbara J. Benson, Carl J. Bowser, John J. Magnuson, and Katherine E. Webster. 1997. The influence of landscape position on northern Wisconsin lakes. *Freshwater Biology* 37:209-217.

Soranno, P. A., K. E. Webster, J. L. Riera, T. K. Kratz, J. S. Baron, P. Bukaveckas, G. W. Kling, D. White, N. Caine, R. C. Lathrop, and P. Leavitt. 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. *Ecosystems* 2:395-410.

Ph.D Advisor: Tim Allen

Recent Collaborators: B. Bojanovsky, D. W. Bolgrien, P.L. Brezonik, W. Y. B. Chang, V. Drabkova, M.J. Gonzalez, B. P. Hayden, D. P. Morris, R.G. Rada, V. Straskrabova, C.J. Watras, J.G. Wiener, C.E. Williamson.

BIOGRAPHICAL SKETCH

MONICA G. TURNER

Department of Zoology, University of Wisconsin, Madison, WI 53706. Tel: (608) 262-2592
Fax: (608) 265-6320 Email: mgt@mhub.zoology.wisc.edu

Born 9 December 1958, New York City, NY

Education

B. S. Biology, 1980, Fordham University, Bronx, New York
summa cum laude, in cursu honorum ; Phi Beta Kappa; New York Regents Scholarship

Ph.D. Ecology, 1985, University of Georgia, Athens, Georgia
with honors; Phi Kappa Phi

Experience

1999- Professor, Department of Zoology, University of Wisconsin
1995 - 99 Associate Professor, Department of Zoology, University of Wisconsin
1994 - 95 Assistant Professor, Department of Zoology, University of Wisconsin
1990 - 95 Adjunct Faculty, Graduate Program in Ecology, University of Tennessee
1989- - 94 Research Staff Scientist, Environ. Sci. Div., Oak Ridge National Lab.
1987 - 89 Hollaender Distinguished Fellow, Environ. Sci. Div., Oak Ridge National Lab.
1985 - 87 Postdoctoral Research Associate Insitute of Ecology, Univ. Georgia

Selected Professional Activities and Awards

1999- Committee on Management of Ungulates in Yellowstone National Park, National Academy of Sciences
1999 Romnes Fellowship, Graduate School, University of Wisconsin-Madison
1998 Distinguished Landscape Ecologist, US-IALE
1997- Ecosystems Panel, National Academy of Sciences
1996- Co-Editor in Chief, Ecosystems (with S. R. Carpenter)
1995- Editorial Board, BioScience
1995-1997 Science Advisory Board, National Center for Ecological Analysis and Synthesis, University of California-Santa Barbara.
1995 Keynote Speaker, International Congress of Landscape Ecology, Toulouse, France
1993-1996 Ecosystems Advisory Panel, National Science Foundation
1994-1996 President, US Assoc., International Association for Landscape Ecology
1994 Distinguished Ecologist Series, Colorado State University
1993 Keynote speaker, The Ecological Role of Fire in the Greater Yellowstone Area,
Yellowstone National Park
1993 Terrestrial Ecology Technical Panel, NASA
1992-95 Editorial Board, Ecological Applications
1992- Editorial Board, Landscape Ecology

BIOGRAPHICAL SKETCH

(This is a continuation page)

1990-1992 Committee on Federal Acquisition of Lands for
Conservation, National Academy of Sciences

1990 Scientific Achievement Award, Environmental Sciences Division, ORNL
1990 Long-term Ecological Research (LTER) Panel, National Science Foundation

Five Publications Most Relevant to Proposed Research (n > 100)

Turner, M. G., R. H. Gardner and R. V. O'Neill. 1995. Ecological dynamics at broad scales. *BioScience: Supplement S-29 to S-35*.

Turner, M. G., D. N. Wear and R. O. Flamm. 1996. Land ownership and land-cover change in the Southern Appalachian Highlands and the Olympic Peninsula. *Ecological Applications* 6:1150-1172.

Wear, D. N., M. G. Turner, and R. J. Naiman. 1998. Institutional imprints on a developing forested landscape: implications for water quality. *Ecological Applications* 8:619-630.

Turner, M. G., S. R. Carpenter, E. J. Gustafson, R. J. Naiman, and S. M. Pearson. 1998. Land use. Pages 37-61 In: M. J. Mac, P. A. Opler, P. Doran, and C. Haecker, editors. Status and trends of our nation's biological resources. Volume 1. National Biological Service, Washington, D.C.

Naiman, R. J. and M. G. Turner. A future perspective on aquatic ecosystems: trends, consequences, and challenges. *Ecological Applications* (In press).

Five Other Publications

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-197.

Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology* 8:213-227.

Turner, M. G., W. H. Romme, R. H. Gardner and W. W. Hargrove. 1997. Effects of patch size and fire pattern on succession in Yellowstone National Park. *Ecological Monographs* 67:411-433.

Gergel, S. E., M. G. Turner, and T. K. Kratz. 1999. Scale-dependent landscape effects on north temperate lakes and rivers. *Ecological Applications* 9:1377-1390.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2000. Pattern and process: landscape ecology in theory and practice. Springer-Verlag, New York (Forthcoming)

Additional Information Requested by NSF

1. Postdoctoral scholars advised by Turner = 6 (total), 4 (current)

BIOGRAPHICAL SKETCH

(This is a continuation page)

Graduate students advised by Turner = 10 (total), 6 (current)

2. Advisors

Frank B. Golley, University of Georgia (Ph.D. advisor)

Eugene P. Odum, University of Georgia (Postdoctoral advisor)

3. Recent collaborators (last 48 months, excluding University of Wisconsin colleagues)

W. H. Baker, University of Wyoming; P. Bohlstad, University of Minnesota; D. C. Coleman, University of Georgia; V. H. Dale, Oak Ridge National Laboratory; R. H. Gardner, Appalachian Laboratory, University of Maryland; E. J. Gustafson, USDA Forest Service; W. W. Hargrove, Oak Ridge National Laboratory; D. H. Knight, University of Georgia; J. Liu, Michigan State University; J. L. Meyer, University of Georgia; R. J. Naiman, University of Washington; R. V. O'Neill, Oak Ridge National Laboratory; S. M. Pearson, Mars Hill College; R. K. Peet, University of North Carolina; C. Peterson, University of Georgia; W. H. Romme, Fort Lewis College; P. Soranno, Michigan State University; T. P. Spies, USDA Forest Service; G. A. Tuskan, Oak Ridge National Laboratory; J. A. Wiens, Colorado State University; K. A. With, Bowling Green State University; D. L. Urban, Duke University; D. N. Wear, USDA Forest Service.

BIOGRAPHICAL SKETCH

CURRICULUM VITAE

Timothy F. Allen

(i) **TIMOTHY F. ALLEN**, Professor of Botany, Department of Botany, University of Wisconsin-Madison, Madison, Wisconsin 53706. Telephone number (608) 262-2692. FAX number (608) 262-2692. Email address: allen@macc.wisc.edu

(ii) **Born:** July 6, 1942, S. Croydon, Surrey, U.K., Permanent U.S. Resident.

(iii) **B.Sc., 1964; Ph.D., 1968, University College North Wales, University of Wales, Bangor, North Wales.**

(iv) **Positions:**

(1) **Demonstrator (TA equivalent), University College North Wales, School of Plant Biology, 1964-1968.**

(2) **Lecturer (Assistant Professor equivalent), Department of Biological Science, University of Ife, Nigeria, 1968-1970.**

(3) **Assistant Professor, Department of Botany, University of Wisconsin-Madison, Wisconsin, 1970-1973.**

Associate Professor, 1973-1981.

Professor 1981-present.

Jointly on faculty of Department of Integrated Liberal Studies, University of Wisconsin-Madison, Wisconsin; 1980-present.

Member of faculty of Institute for Environmental Studies, Conservation and Land Management Programs.

(4) **Visiting Professor, Department of Anthropology and Cybernetic Systems, San Jose State 1988-89.**

B) Five most pertinent publications:

(1) **Ahl, V.A. and T.F.H. Allen. 1996. Hierarchy theory: a vision vocabulary and epistemology. Columbia. NYC.**

(2) **Allen, T.F.H., A. King, A. Johnson, B. Milne, and S. Turner. The problem of scaling in ecology. *Evol. Trends in Plants*. 7:3-8.**

(3) **Allen, T.F.H. and T.W. Hoekstra. 1991. The role of heterogeneity in scaling of ecological systems under analysis. Chapter 3 in J. Kolasa and S. Pickett eds. Springer-Verlag, pp. 47-68.**

(4) **Allen, T.F.H., and R.V. O'Neill. 1991. Improving predictability in networks: system specification through networks, pp. 101-114. In: M. Higgashi and T.P. Burns (eds) *Theoretical studies of ecosystems: the network perspective*, pp. 364, Cambridge.**

(5) **Allen, T.F.H. and T.W. Hoekstra. 1992. *Towards a unified ecology*, Columbia Univ. Press.**

Five other publications:

BIOGRAPHICAL SKETCH

(This is a continuation page)

(1) Beland, P. and T.F.H. Allen. 1994. The origin and evolution of the genetic code. *J. Theor. Biol.* 170:359-365.

(2) Allen, T.F.H. and T.W. Hoekstra. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. *Journal of Vegetation Science* 1: 5-12.

(3) Hoekstra, T.W., T.F.H. Allen and C.H. Flather. 1991. The implicit scaling in ecological research: on when to make studies of Mice and Men. *Bioscience* 41: 148-154.

(4) Allen, T.F.H. and T.B. Starr. 1982. *Hierarchy: Perspectives for ecological complexity.* (University of Chicago Press, pp. 310).

(5) O'Neill, R.B., D. DeAngelis, J.B. Waide and T.F.H. Allen. 1986. A hierarchical concept of ecosystems. *Monographs in population biology* 23. Pp. 272. Princeton.

C) Scientists with whom I have worked recently and who would be in conflict in review:
C. Allen, S. Appolonio, M. Bevers, G. Bradshaw, Y. Cohen, C. Curtin, L. Dickie, R. Gardner, T. Hoekstra, J. Hof, A. Johnson, J. Kay, S. Kerr, C. Kibert, B. Milne, G. Mitman, T. Parker, J. Pastor, B. Patten, D.L. Peterson, G. Peterson, D. Roberts, E. Rykiel, J. Sendzmir, J. Tainter, R. Ulanowitz, S. Wolf.

Major Professor: the Late N. Woodhead

D) M.S. and Ph.D. students I have graduated: S.M. Bartell, W.M. Post, R. Kimmerer, D. Sadowsky, A. Prunty, B. Schnee, M. Burd, E. Knox, T. Kratz, B. Reynolds, B. McCune, M. Fulton, M. Stevens, C. Dott, B. Sherman, D. Einstein, C. Toney, L. Puth.

BIOGRAPHICAL SKETCH

Biographical Sketch for Thomas M. Frost

A. Address

Trout Lake Station, Center for Limnology, University of Wisconsin, 10810 County N, Boulder Junction, WI 54512. Phone 715-356-9494, Fax 715-356-6866. Email: tfrost@facstaff.wisc.edu).

Personal Data

Born 2 July 1950 in Darby, Pennsylvania, U.S.A.
Married with 2 children.

Education

B.S. (Biology), 1973, Drexel University, Philadelphia, Pennsylvania.

Ph.D. (Biology), 1978, Dartmouth College, Hanover, New Hampshire. Thesis: The ecology of the freshwater sponge *Spongilla lacustris*. Advisor: John J. Gilbert

Employment

Sept. 1999-present. Associate Director for Trout Lake Station and Senior Scientist, Center for Limnology, University of Wisconsin-Madison.

Sept. 1997-Aug. 1999. Program Officer, Ecology, National Science Foundation

July 1981-Aug. 1997. Associate Director for Trout Lake Station, Center for Limnology, University of Wisconsin-Madison.

Current Funding

National Science Foundation - Long-Term Studies Program. 1 November 1996 - 31 October 2002. Comparative Studies of a Suite of Lakes in Wisconsin. Co-Principal investigator with Steve Carpenter and other researchers. \$6,00,00 (DEB - 9632853).

National Science Foundation. 1 January 1999 - 31 January 2001. LTREB: Continuing Assessment of Ecological Recovery Following Experimental Acidification of Little Rock Lake, Wisconsin \$117,586 (IBN - 9815519).

B. Five Papers Most Related to Proposal.:

Frost, T.M., P.K. Montz, T.K. Kratz, T. Badillo, P.L. Brezonik, M. J. Gonzalez, R. G. Rada, C. J. Watras, K.E. Webster, J. G. Wiener, C.E. Williamson and D P. Morris. 1999. Multiple stresses from a single agent: diverse responses to the experimental acidification of Little Rock Lake, Wisconsin. *Limnology and Oceanography* 44: 784-794.

Frost, T. M., P. K. Montz, M. J. Gonzalez, B. L. Sanderson, and S.E. Arnott. 1999. Rotifer responses to increased acidity: long-term patterns during the experimental manipulation of Little Rock Lake. In *Rotifera VIII: A comparative Approach* (E. Wurdak, R. Wallace and H. Segers, eds). *Hydrobiologia* 387/388: 141-152.

BIOGRAPHICAL SKETCH

(This is a continuation page)

Lukaszewski, Y., S.E. Arnott and T.M. Frost. 1999. Regional versus local processes in determining zooplankton community composition of Little Rock Lake, Wisconsin, USA. *Journal of Plankton Research* 21: 991-1003.

Frost, T.M., P.K. Montz, and T.K. Kratz. 1998. Zooplankton community responses during recovery from acidification: limited persistence by acid-favored species in Little Rock Lake, Wisconsin. *Restoration Ecology* 6: 336-342.

Frost, T.M., S.R. Carpenter, A. R. Ives, and T.K. Kratz. 1995. Species compensation and complementarity in Ecosystem Function. pages 224-239 in (C.G. Jones and J.H. Lawton eds.) *Linking Species and Ecosystems*, Chapman and Hall, New York. 387pp.

Five Other Papers:

Frost, T.M. and J.M. Fischer. (in press) Assessing the effects of acidification on aquatic ecosystems. In: Sala, O., R. Jackson, H. Mooney, and R. Howarth, eds., *Methods in Ecosystem Science*. Springer, in press.

Frost, T.M., H. M. Reiswig, and A. Ricciardi in press. Porifera. Pages xxx-xxx in J. H. Thorp and A. P. Covich, editors. *Ecology and Classification of North American Freshwater Invertebrates (Second Edition)*. Academic Press, New York, New York, USA.

Descy, J.-P., T.M. Frost and J.P. Hurley. 1999. Assessments of grazing by the freshwater copepod *Diatomus minutus* using carotenoid pigments: a caution. *Journal of Plankton Research* 21: 127-145.

Colby, A.C.C, T.M. Frost, and J.M. Fischer. 1999. Sponge distribution and lake chemistry in northern Wisconsin lakes: Minna Jewell's survey revisited. *Memoirs of the Queensland Museum* 44: 93-99. Brisbane. ISSN 0079-8835.

Fischer, J.M., and T.M. Frost. 1997. Indirect effects of lake acidification on *Chaoborus* population dynamics: the role of food limitation and predation. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 637-646.

C. Collaborators not listed on publications: Alan Covich, Kathy Cottingham, Brian Dennis, Robert Gardner, Subhash Lele, Jean Miller, Mike Patterson, Mark Taper, Tim Wootton and Norm Yan.

D. Graduate Advisees: Michael Sierszen, Daniel Schneider, Maria Gonzalez, Beth Sanderson, Janet Fischer, and Shelley Arnott.

Postdoctoral Associate: Rita Adrian

E. Graduate Advisor: John J. Gilbert, Postdoctoral Advisor: William M. Lewis, Jr.

BIOGRAPHICAL SKETCH

Sara C. Hotchkiss: Biographical Sketch

Address: Department of Geology and Geophysics, University of Wisconsin, Madison, WI 53706. Tel. 608-265-5796. Email: sara@geology.wisc.edu. FAX: 608-262-0693.

Education: B.A. 1987, Biology, Oberlin College, Oberlin, OH.; Ph.D. 1998, Ecology/Quaternary Paleocology, University of Minnesota-Twin Cities.

Appointments: Postdoctoral Research Associate, Stanford University, 1998-present; Assistant Scientist, Department of Geology and Geophysics, University of Wisconsin, 1998-present.

Professional Activities (selected): Member of Ecological Society of America, American Quaternary Association, Geological Society of America, American Geophysical Union; Reviewer for Biogeochemistry, Ecology/Ecological Monographs, Journal of Paleolimnology.

Selected Honors: Buell Award for Excellence in Ecology, Ecological Society of America, 1996; Deevey Award for best student presentation, Paleocology Section of the Ecological Society of America, 1996; Gaudreau Award for Excellence in Quaternary Science, American Quaternary Association, 1996-1997.

Publications Related to This Proposal

Hotchkiss, S.C. and J.O. Juvik. 1999. A Late-Quaternary pollen record from Ka'au Crater, O'ahu, Hawai'i. *Quaternary Research* 52: 115-128.

Nullet, D., Fletcher, C.H., III, Hotchkiss, S., and Juvik, J.O. 1998. Paleoclimate and geography. Pages 64-66 in *Atlas of Hawai'i*. Juvik, S.P. and Juvik, J.O, eds. University of Hawai'i Press, Honolulu.

Hotchkiss, S.C. 1998. Quaternary vegetation and climate of Hawai'i. Ph.D. dissertation, University of Minnesota, Saint Paul.

Collaborators in Past 48 Months (In addition to advisees and Co-PIs of this proposal): R. Calcote, O.A. Chadwick, C. Douglas, D. Foote, T. Giambelluca, J. Juvik, E. Karlin, L. Loope, E.A. Lynch, D. Mladenoff, J. Price, V. Radeloff, P.M. Vitousek.

Graduate Advisor: M.B. Davis.

BIOGRAPHICAL SKETCH

James F. Kitchell: Biographical Sketch

Address: Center for Limnology, 680 N. Park St., University of Wisconsin, Madison, WI 53706. Tel.: 608-262-9512. Email: KITCHELL@MACC.WISC.EDU. FAX: 608-265-2340.

Personal: Born Gary, IN, 20 July 1942; U.S. citizen; married, two children.

Education: B.S., Biology, Ball State Teachers College, Muncie IN, 1964. Ph.D., Biology, University of Colorado, Boulder CO, 1970

Positions: Project Associate and Assistant Scientist, Inst. Env. Stud. (1970-74), Assistant Professor (1974-77), Associate Professor (1977-82), and Professor (1982-) Department of Zoology, University of Wisconsin, Madison, Wisconsin; Associate Director, Center for Limnology (1985-present); Acting Director, Center for Limnology (1985-86, 1992); A. D. Hasler Professor (1995-present),

Selected Professional Activities: Member, NAS Board on Environmental Science and Technology (1999-), Coordinator, Living Resources Program, Univ. Wisconsin Sea Grant (1981-); National Marine Fisheries Service Ecosystem Principles Advisory Panel (1997-99); President, Association Ecosystem of Research Centers (1994-95); Chair, Oceanography and Limnology Graduate Program, UW-Madison (1991-94); Editorial Board, Fishery Bulletin (1986-90); Advisory Panels for NSF Programs: Long Term Ecological Research/Land-Ocean Margin Ecosystems (1999), Field Stations and Marine Laboratories (1993-96, 1999), Research Training Grants (1991), Science and Technology Centers (1989), Long Term Ecological Research (1987-88), Ecosystem Studies (1984-86).

Instructional Activities: Fall Semesters; Problems in Oceanography (Zool./Bot./IES/Geol & Geophysics, Atmos. & Oc. Sci./Civil and Env. Engin. 750), Limnology Seminar (Zoology 955) Spring Semesters: Ecology of Fishes Lecture (Zoology 510), Ecology of Fishes Laboratory (Zoology 511), Conservation Biology (Bot./IES/Wildlife Ecol./Zool. 651).

Five Publications Closely Related to this Proposal (Total = 138 since 1968, including two books)

Harvey, C.J., and J.F. Kitchell. A stable isotope evaluation of the structure and spatial heterogeneity of a Lake Superior food web. *Can. J. of Fish. Aquat. Sci.*: In press.

Essington, T. E., and J. F. Kitchell. 1999. New perspectives in the analysis of fish distributions: A case study on the spatial distribution of largemouth bass. *Can. J. Fish. Aquat. Sci.* 56:1-9.

Post, D. M., J. F. Kitchell and J. R. Hodgson. 1998. Interactions of spawning date, growth rates, predation and overwinter mortality in largemouth bass recruitment. *Can. J. Fish. Aquat. Sci.* 55: 2588-2600.

Kitchell, J. F., E. A. Eby, X. He, D. E. Schindler and R. M. Wright. 1994. Predator-prey dynamics in an ecosystem context. *J. Fish Biol.* 45:209-226.

Carpenter, S.R., and J.F. Kitchell (eds.). 1993. *The Trophic Cascade in Lakes*.

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Cambridge Univ. Press, Cambridge, England.

Five other significant publications:

Kitchell, J. F., C. Boggs, X. He and C. J. Walters. 1999. Keystone predators in the Central Pacific. Pages 665-683 In Proc. 12th Wakefield Symposium on Ecological Considerations in Fisheries Management. Univ. of Alaska Sea Grant, Anchorage, Alaska. 756 pp.

Walters, C. J., D. M. Pauly and J. F. Kitchell. Representing density dependent consequences of life history strategies in an ecosystem model: ECOSIM II. Ecosystems: In press.

Pace, M. L., J. J. Cole, S. R. Carpenter and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483-488.

Kitchell, J. F., D. E. Schindler, B. R. Herwig, D. M. Post, M. H. Olson and M. Oldham. 1999. Nutrient cycling at the landscape scale: The role of diel foraging migrations by geese at the Bosque del Apache Wildlife Refuge, New Mexico. Limnology and Oceanography 44:828-836.

Kitchell, J.F. (ed.). 1992. Food Web Management: A Case Study of Lake Mendota. Springer-Verlag, New York. 553 p.

Graduate Students (1992-): Daniel Schindler (M.S. 1992), Brett Johnson (Ph.D. 1993), Russell Wright (Ph.D. 1993), Timothy Johnson (Ph.D. 1995), Lisa Eby (M.S. 1995), Daniel Schindler (Ph.D. 1995), David Post (M.S. 1996), Timothy Essington (Ph.D. 1999). Current Graduate Students: Christofer Harvey, Jefferson Hinke, Brian Roth, Greg Sass.

Postdoctoral Trainees (1992-): Lars Rudstam (1988-92), Patricia Sanford (1987-93), Xi He (1990-94), Mark Olson (1993-96), Doran Mason (1994-97), Daniel Schindler (1996-97), Timothy Johnson (1995-98), Timothy Essington (1999-).

Collaborators in Past 48 Months (In addition to advisees, co-authors and Co-PIs of this proposal):

James Breck, Roy Stein, Gary Fahnenstiel, Jack Mattice, Robert Otto, David Lodge, Craig Sandgren, Robert Hecky, Sally MacIntyre, Ann Giblin, George Kling, John Lehman, James Rice, Larry Crowder, members of National Marine Fisheries Service Ecosystem Principles Advisory Panel, members of the NSF panels on Field Stations/Marine Laboratories and LTER/LOME.

Graduate Advisor: J. T. Windell (retired)

BIOGRAPHICAL SKETCH

John J. Magnuson: Biographical Sketch
Updated 24 February, 2000

Address: Center for Limnology, University of Wisconsin - Madison, Madison, Wisconsin 53706. Tel. 608-262-3014. Email: jmagnuson@mhub.limnology.wisc.edu. FAX: 608-265-2340.

Personal: born Evanston IL, 8 March 1934; U.S, citizen; married, two children

Professional Preparation: B.Sc. with distinction, 1956, Fish & Wildlife Management, University of Minnesota, M.Sc., 1958, Fish & Wildlife Management, University of Minnesota, Ph.D., 1961, Zoology/Oceanography, University of British Columbia, Vancouver B.C. Canada.

Appointments: Assistant to Full Professor of Zoology 1968-present, Director of Center for Limnology 1983-present, Chief Tuna Behavior & Physiology Program, US Bureau of Commercial Fisheries HA, 1961-7.

Synergistic Activities (selected): Intergovernmental Panel on Climate Change, 2nd Assessment - a convening lead author of Hydrology and Freshwater Ecology -1995, a lead Author on Ecosystems - lakes and streams. National Research Council, (Committee chair) Protection and Management of Pacific Northwest Anadromous Salmonids 1992-5; Assessment of Atlantic Bluefin Tuna 1994; Improving the Management of U.S. Marine Fisheries 1993-94; Sea Turtle Conservation 1989-90. International Joint Commission Great Lakes Water Quality-Science Advisory Board, 1990-95. National Science Foundation, Program Director for Ecology 1975-96. Ecological Society of America, Editorial Board for Ecological Applications, 1989-94. Freshwater Imperative, co-chair with Bob Naiman, 1992-95: NSF-sponsored workshop and Publication

Selected Honors: National Science Foundation Midcareer Fellowship, University of Washington, 1992. Fellow - American Association for the Advancement of Science 1966. Wisconsin Idea Award in Natural Resource Policy, University of Wisconsin-Madison Center for Resource Policy Studies and Programs, 1990.

Five Publications Closely Related to This Proposal (from >300 research papers and 2 books since 1962)

Magnuson, J.J. 1976. Managing with exotics--A game of chance. *Trans. Am. Fish. Soc.* 105(1):1-9.

Lorman, J.G. and J.J. Magnuson. 1978. The role of crayfish in aquatic ecosystems. *Fisheries* 3(6):8-10.

Magnuson, J.J., B.J. Benson, and A. S. McLain. 1994. Insights on species richness and turnover from long-term ecological research: Fishes in north temperate lakes. *Am. Zool.* 34:437-451.

Magnuson, J.J., W.M. Tonn, A. Banerjee, J. Toivonen, O. Sanchez, and M. Rask. (1998). Isolation vs. extinction in the assembly of fishes in small northern lakes. *Ecology* 79(8): 2941-56.

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Hrabik, T. R., J. J. Magnuson, and A. S. McLain. 1998. Predicting the effects of rainbow smelt on native fishes: evidence from Long-term research on two lakes. *Can. J. Fish. Aquat. Sci.* 55: 1364-1371.

Five Additional Publications

Magnuson, J.J., L.B. Crowder and P.A. Medvick. 1979. Temperature as an ecological resource. *Am. Zool.* 19:331-43.

Magnuson, J.J. 1990. Long-term ecological research and the invisible present. *BioScience* 40(7):495-501.

Magnuson, J.J. 1991. Fish and fisheries ecology. *Ecological Applications* 1(1):13-26.
Magnuson, J.J., K.E. Webster, R. A. Assel, C.J. Bowser, P.J. Dillon, J.G. Eaton, H. E. Evans, D.J. Fee, R. I. Hall, L.R. Mortsch, D.W. Schindler, and F.H. Quinn. 1997. Potential effects of climate change on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. pp 7-53 in C.E. Cushing [ed] *Freshwater Ecosystems and climate change in North America, A regional Assessment. Advances in Hydrological Processes.* John Wiley & Sons viii. + 262pp. (Also as an Issue of the *Journal Hydrological Processes* 11(6) 1997.)

Magnuson, J.J. and T.K. Kratz. (In Press). Lakes in the landscape: approaches to regional limnology. *Verh. Internat. Verein. Limnol.*

Collaborators in Past 48 Months (In addition to advisees and Co-PIs of this proposal): D. Armstrong, C.B. Bowser, J. Gosz, E. Houde, K. Lee, D.M. Lodge, H. Mooney, R.J. Naiman, D. Policansky, D.M. Robertson, J.C. VandeCastle, N.D. Yan.

Advisees (graduate and postdoctoral): S. E. Arnott, S.B. Baines, D. Bolgrien, S.B., Brandt, J.C. Brazner, G.M. Capelli, L. B. Crowder, B.T. DeStasio, T.R. Hrabik, J. Fischer, J. Lenters, J.G. Lorman, J. Lyons, A.S. McLain, K. Mills, J. A. Nelson, F. J. Rahel, J. Riera, L.G. Rudstam, B. Sanderson, R.A. Stein, W.M. Tonn, M.J. Weaver, K.E. Webster, R.W. Wynne.

Graduate Advisors: Deceased

BIOGRAPHICAL SKETCH

Bill Provencher: Biographical Sketch
(updated 24 February, 2000)

Address: Department of Agricultural and Applied Economics, University of Wisconsin, Madison, WI 53706. Tel. 608-262-9494. Email: PROVENCHER@AAE.WISC.EDU. FAX: 608-262-4376.

Professional Preparation: B.S. 1981, Natural Resources, Cornell University; M.S. 1985, Forestry, Duke University; Ph.D., 1991, Agricultural Economics, University of California-Davis.

Appointments: Instructor, Department of Agricultural and Applied Economics, University of Wisconsin-Madison, 1990-1991; Assistant Professor to Associate Professor, Department of Agricultural and Applied Economics, University of Wisconsin-Madison, 1991-present.

Synergistic Activities (selected): Editorial Board, Land Economics; Editorial Council, Journal of Environmental Economics and Management.

Publications Closely Related to This Proposal

Provencher, B. 1997. Structural versus Reduced-Form Estimation of Optimal Stopping Problems, *American Journal of Agricultural Economics* 79, 357-368.

Provencher, B. and R.C. Bishop. 1997. An Estimable Dynamic Model of Recreation Behavior with an Application to Great Lakes Fishing, *Journal of Environmental Economics and Management*, 33, 107-127.

Five Additional Publications

Provencher, B. 1995. An Investigation of the Harvest Decisions of Timber Firms in the South-East United States, *Journal of Applied Econometrics* 10, 57-74.

Provencher, B. 1995. Structural Estimation of the Stochastic Dynamic Decision Problems of Resource Users: An Application to the Timber Harvest Decision, *Journal of Environmental Economics and Management* 29, 321-338.

Provencher, B. and O.R. Burt. 1994. A Private Property Rights Regime for the Commons: the Case of Groundwater, *American Journal of Agricultural Economics* 76, 875-888.

Provencher, B. and O.R. Burt. 1994. Approximating the Optimal Groundwater Pumping Policy in a Multiaquifer Stochastic Conjunctive Use Setting, *Water Resources Research* 30, 833-843.

Provencher, B. and O.R. Burt. 1993. The Externalities Associated with the Common Property Exploitation of Groundwater, *Journal of Environmental Economics and Management* 24, 139-158.

Collaborators in Past 48 Months (In addition to advisees and Co-PIs of this proposal):
R.C. Bishop, D. W. Marcouiller

Advisees (graduate and postdoctoral): K.A. Baerenklau, M. Bennett, W.M. Clune, B. Demeke,

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J.C. McPeak, B. Rosenthal, F.A. Spalatro

Graduate Advisor: O.R. Burt

BIOGRAPHICAL SKETCH

Eric W. Triplett: Biographical Sketch
(updated 7 February, 2000)
(full CV at <http://agronomy.wisc.edu>)

Address: University of Wisconsin-Madison, Department of Agronomy, 1575 Linden Drive, Madison, WI 53706. Tel. 608-262-9824. Email: triplett@facstaff.wisc.edu. FAX: 608-262-5217.

Personal: born Philadelphia, PA, 11 July 1954; U.S. citizen; married, two children
Professional Preparation: B.S., High Honors, 1976, Biology, Rutgers University, Cook College, New Brunswick, NJ; M.S., 1978, Botany, University of Maryland, College Park; Ph.D., 1981, Agronomy, University of Missouri, Columbia; Postdoctorate, 1981-1982, Biochemistry, University of Wisconsin-Madison.

Appointments: Assistant Professor, Plant Pathology Department, University of California, Riverside, 1982-1987; Assistant Professor to Professor, Agronomy Department, University of Wisconsin-Madison, 1987-present.

Research Program: Environmental microbiology and molecular plant-microbe interactions: Microbial diversity in lakes, soil, and rhizosphere; analysis of role of endophytic prokaryotes in grasses; mechanism of plant disease suppression conferred by *Burkholderia vietnamiensis* AMMDR1; role and genetic analysis of peptide antibiotic production by *Rhizobium*.

Teaching Program: Teach the genetics portion of introductory biology for majors every spring semester; teach nitrogen metabolism portion of plant biochemistry every fall semester; participate in a seminar for the Center for the Study of Nitrogen Fixation. Offer a graduate course in biological nitrogen fixation.

Professional Activities (selected): Editorial Board, Applied and Environmental Microbiology; Associate Chair, Department of Agronomy, 1995-present; Faculty Senator; Chair, Steenbock Library Committee.

Publications (10) most closely related to this proposal (55 research papers and 1 book since 1980)

Chelius, M.K. and E.W. Triplett. 2000. *Dyadobacter fermentans* gen. nov., sp. nov., a novel gram-negative bacterium isolated from surface-sterilized *Zea mays* stems. *Inter. J. System. Bacteriol.* (in press).

Chelius, M.K. and E.W. Triplett. 2000. Diazotrophic endophytes associated with maize. In: *Prokaryotic Nitrogen Fixation: a Model System for the Analysis of a Biological Process*, E.W. Triplett, ed., Horizon Scientific Press, Norfolk, UK, pp. 779-792.

Chelius, M.K. and E.W. Triplett. 2000. Immunolocalization of dinitrogenase reductase produced by *Klebsiella pneumoniae* in association with *Zea mays* L. *Appl. Environ. Microbiol.* 66:783-787.

Fisher, M.M. and E.W. Triplett. 1999. Automated approach for ribosomal intergenic spacer analysis of microbial diversity and its application to freshwater bacterial communities.

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Appl. Environ. Microbiol. 65:4630-4636.

Chelius, M.K. and E.W. Triplett. 1999. Rapid detection of endomycorrhizal fungi in roots and soil of an intensively managed turfgrass system by PCR amplification of small subunit rDNA. Mycorrhiza 9:61-64.

Robleto, E.A., J. Borneman, and E.W. Triplett. 1998. Effects of bacterial antibiotic production on rhizosphere microbial communities from a culture independent perspective. Appl. Environ. Microbiol. 64:5020-5022.

Robleto, E.A., K. Kmiecik, E.S. Oplinger, J. Nienhuis, and E.W. Triplett. 1998. Trifolitoxin production increases nodulation competitiveness of *Rhizobium etli* CE3 under agricultural conditions. Appl. Environ. Microbiol. 64: 2630-2633.

Borneman, J. and E.W. Triplett. 1997. A rapid and direct method for extraction of RNA from soil. Soil Biol. Biochem. 29:1621-1624.

Borneman, J. and E.W. Triplett. 1997. Molecular microbial diversity in soils from eastern Amazonia: evidence for unusual microorganisms and population shifts associated with deforestation. Appl. Environ. Microbiol. 63:2647-2653.

Borneman, J., P.W. Skroch, J.A. Jansen, K.L. O'Sullivan, J.A. Palus, N.G. Rumjanek, J. Nienhuis, and E.W. Triplett. 1996. Microbial diversity of an agricultural soil in Wisconsin. Appl. Environ. Microbiol. 62:1935-1943.

**Recent Collaborators (last 48 months), other than those cited in publications:
S. Kaeppler, J. Parke, D. Armstrong, J. Sims, A. Edison, A. Gargas, K. Albrecht, M. Casler, S. Carpenter, T. Kratz, L. Graham, D. Armstrong.**

Graduate Students (1996-)

Angela Kent (PhD 2000, expected), Alexandra Scupham (PhD 2000, expected), Marisa Chelius (PhD 1999), Eduardo Robleto (PhD 1998), Brenda Breil (PhD 1996)

Postdoctoral Trainees (1996-)

Marisa Chelius (1999-present), Tom Herlache (1999-present), Yuemei Dong (1999-present), Madeline Fisher (1998-present), Eduardo Robleto (1998-1999), James Borneman (1995-97), Victor Rumjanek (1996).

Graduate and Post doctoral Advisor

Dale Blevins, PhD advisor, University of Missouri, Columbia

Paul Ludden, Postdoctoral advisor, University of Wisconsin-Madison