COMPARATIVE STUDY OF A SUITE OF LAKES IN WISCONSIN

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Section 1. Project Summary

Lakes are central to the vitality of landscapes and society. As collectors of water, energy, solutes, and pollutants from the landscape and atmosphere, as habitats for aquatic biota, and as attractors of human activities, lakes affect and are affected by natural and human-induced changes in the local and regional landscape and atmosphere. The North Temperate Lakes Long-Term Ecological Research program seeks to understand the long-term ecology of lakes and their interactions with a range of relevant landscape, atmospheric, and human processes. Our program has the following five, interrelated goals.

1. Perceive long-term changes in the physical, chemical, and biological properties of lake ecosystems.
2. Understand interactions among physical, chemical, and biological processes within lakes and their influences on lake characteristics and long-term dynamics.
3. Develop a regional understanding of lake ecosystems through an analysis of the patterns and processes organizing lake districts.
4. Develop a regional understanding of lake ecosystems through integration of atmospheric, hydrologic and biotic processes.
5. Understand the way human, hydrologic, and biogeochemical processes interact within the terrestrial landscape to affect lakes and the way lakes, in turn, influence these interactions.

We examine patterns, processes, and interactions of lakes and their surroundings at a nested set of spatial and temporal scales. Spatially, we focus on four scales: individual lakes, multiple neighboring lakes, entire lake districts, and the Upper Great Lakes region. Temporally, we consider scales of within-year, among-years, decades, and centuries. We use multiple approaches, including long-term observations, comparative studies, experimental manipulations, and process modeling. Our research group includes ecologists, geologists, chemists, demographers, historians, rural sociologists, climatologists, and remote sensing and data management specialists.

We expect our research to produce new conceptualizations of lake dynamics at local to regional scales. These conceptualizations will include understanding the importance of spatial positioning of lakes in a landscape, the feedback between human and lake processes, and the influence of climate and land-use change on lakes.

Collectively, the understanding of landscape-lake-human interactions developed through our LTER research program will have direct relevance to development of policies affecting the future of the Upper Great Lakes Region and enhancement of the quality of life of its residents.

Section 2. Results of Prior Support

Comparative Studies of a Suite of Lakes in Wisconsin

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The North Temperate Lakes Long-Term Ecological Research (NTL-LTER) site was established in 1981. Over the past 15 years we have designed and implemented a comprehensive study of seven lakes in a forested landscape within the Northern Highland Lake District of northern Wisconsin. In November 1994, we used NSF's augmentation of our site and additional state of Wisconsin matching funds to add four study lakes in agricultural and urban catchments in southern Wisconsin, increase our breadth by adding social scientists to our research group, and increase the regional significance of our findings by supporting extensive interactions with researchers at two Canadian lake research sites.

As evidenced by the 161 peer-reviewed publications produced during 1990-1995, we have made significant advances in the understanding of lake ecology (Figure 1 and attached publication list). The listed publications include papers and theses by LTER investigators and other investigators who have used our data, and synthetic as well as policy-oriented publications generated from interactions involving our LTER scientists.

Prior results have a similar breadth of perspective as does our proposed research. Using information from our long-term database, we studied the ecology of lakes by considering in-lake processes, interactions between lakes and their surrounding environment, lake-landscape relationships within regions, and human-lake interactions. For brevity, only a few, representative examples are covered here. Others are shown in proposed research and our publication list.

Long Term Data and their Management

We collect and manage high-quality, comprehensive, long-term datasets on the physical, chemical, and biological properties and processes of the LTER lakes and the surrounding landscape (Magnuson and Bowser 1990, Kratz et al. 1986). All of these data are available electronically to LTER investigators and collaborators and subsets are published on the World Wide Web (Table 1). The number of data requests and access history of our web page are summarized in Table 2. Data management at our site is described in more detail in Section 5: Data and Information Management.

In-Lake Processes

- *Invasion of Exotics*: Two notable exotics, rusty crayfish and rainbow smelt, have invaded the northern Wisconsin LTER lakes since our study began. Crayfish greatly modified the macrophyte community and altered the functioning of the littoral zone (Lodge 1991). Smelt invaded the pelagic zones and through predation have caused the extirpation of a native planktivore (cisco) in one lake (McLain 1991), and through competition have greatly reduced the growth of yellow perch in another lake (Hrabik 1995) (Figure 2).

- *Algal Population Regulation*: We studied factors regulating aspects of algal dynamics in northern and southern Wisconsin lakes. In the north we hypothesized that dinoflagellate population differences in two LTER bog lakes (Crystal Bog and Trout Bog) could be attributed to population growth or loss processes. Unexpectedly, the interplay between basin morphology and the emergence of resting stages from sediments explained the difference (Sanderson and Frost in press). In the south, we analyzed blue green algal dynamics at two time scales in Lake Mendota. Daily concentrations of blue-green algae during summer stratification were best predicted by rainfall, irradiance and wind velocity (Soranno 1995). A stochastic model that predicts annual frequency distributions of blue-green algae from spring total P was developed using data for 1976-1995 (Stow et al. 1996).

- *Nutrient Recycling and Availability*: Based on sedimentation data, recycling within the water column serves as the primary source of N and P for annual production in several of our study lakes (Soranno 1995, Poister et al. 1994). Among-lake patterns in seasonality of production are influenced strongly by population processes of large siliceous algae that sink and efficiently remove nutrients from the water column (Poister et al. 1994).

- *Acid Stress*: The Little Rock Lake Experimental Acidification Project provides an example of collaborative research substantially facilitated but not directly supported by NTL-LTER. The lake's treatment basin was acidified to pH 4.7 in three stages (Figure 3). NTL-LTER data were combined with information from Little Rock Lake's reference basin to evaluate responses to acidification (Carpenter et al. 1991, Brezonik et al. 1993) which were subsequently compared with other large-scale acidification experiments (Schindler et al. 1991). Populations of individual zooplankton species responded dramatically to acidification (Frost et al. 1992); many responses could not have been predicted from laboratory bioassays (Eaton et al. 1992, Gonzalez and Frost 1994). Compared with species composition, total biomass of zooplankton responded slowly (Figure 4) indicating functional compensation in the assemblage (Frost et al. 1995). Following acidification we observed a substantial delay between fast chemical (Figure 3) and slow biological recovery (Figure 4).

- *Grazing and Phosphorus Effects on Phytoplankton*: Analysis of Lake Mendota Secchi disk transparencies, P levels, and food web structure from 1900-1993 revealed strong, additive effects of both grazing and P (Lathrop et al. 1996). Summer transparency improves from 1 m to 3 m when small daphnids are replaced by large ones and P loads are reduced by below-average rainfall. Synthesis of long-term records from Lake Mendota shows that planktivory by cisco can shift the daphnid assemblage from large-bodied to small-bodied species (Johnson 1995). However, the lake's two other major planktivores, yellow perch and white bass, are not capable of causing a shift in daphnid size.

Interactions Between Lakes and their Surroundings

- *Groundwater/Lake Interactions*: We used stable isotopes and numerical modelling to quantify groundwater input to lakes in the Trout Lake area (Krabbenhoft et al. 1990a,b, Bowser 1992, Kenoyer and Bowser 1992a,b, Anderson and Cheng 1993, Cheng and Anderson 1993, Krabbenhoft et al. 1994). Our lakes, characteristic of the region, receive 0 to 40 % of their water from groundwater and the remainder from direct precipitation (Ackerman 1993, Michaels 1995)

- *Ice Phenology and Climate Change*: Lake ice phenologies provide the longest continuous record linking limnology and climate. Lake ice cover data were analyzed as indicators of past and future climate at local to regional scales, including large portions of the Laurentian Shield (Robertson et al. 1992, Wynne and Lillesand 1992, Wynne and Lillesand 1993, Assel and Robertson 1995, Anderson et al. 1996, Wynne et al. 1996)(Figure 5). Using records for the Lake Mendota area, we found that winters have warmed by 2.5(C since 1843 and that ice duration is strongly influenced by El Ni-o events.

- *Thermal Habitat and Climate Change*: The consequences of climatic change for temperate lake physics, chemistry, and ecology are potentially significant (DeStasio et al. 1996, Magnuson and DeStasio 1996, Magnuson et al. 1995, Magnuson et al. 1996a,b, Webster et al. 1996, Vavrus et al. 1996). In collaboration with Australian limnologists, we used output of General Circulation Models based on 2X CO2 scenarios as input to lake physical limnological models (Dynamic Reservoir Simulation Model - DYRESEM), and used the altered lake physics to simulate changes in lake ecology. With the exception of coldwater fish in the smallest lakes, all thermal guilds of fishes had an increase in thermal habitat with warming scenarios (Figure 6).

- *CO2 Dynamics*: We identified and roughly quantified the role that surface waters play as conduits for terrestrially fixed carbon to the atmosphere (Cole et al. 1995). In most lakes we documented annual net movement of carbon from the lake to the atmosphere. This was especially important in dystrophic lakes (Hope et al. in review).

- *Paleolimnology of Silica*: We developed a new paleolimnological technique to evaluate a lake's historic silica concentrations using sponge spicules (Kratz et al. 1991a). Lakes in the Northern Highlands Lake District underwent substantial declines in silica concentrations over the last 10,000 years (Figure 7) perhaps because of changes in weathering rates caused by depletion of easily-weathered, fine particles.

Lake-Landscape Considerations

- *Organization of Lake Districts*: We have begun to develop a conceptual framework for lakes that combines aspects of the river continuum (Vannote et al. 1980) and stream order concepts to explain spatial heterogeneity of lakes across a landscape (research area 3b, below). Groundwater flow is a key factor linking landscape position and lake structure and function (Magnuson et al. 1990, 1991, Kratz et al. 1991b, 1994, 1995, in review).

- *Species Dynamics of Lakes as Islands*: We have begun to elucidate the dynamics of species richness and assemblage structure in inland lakes (McLain and Magnuson 1988, Tonn et al. 1990, Magnuson et al. 1994, Arnott et al. MS). We find that lakes appear more open to invasion and seem better described by metapopulation processes than their island appearance would suggest (research area 3c, below). Among-lake heterogeneity in fish assemblages is only slightly greater than within-lake heterogeneity (Benson and Magnuson 1992)

- *Advances in the Use of Remote Sensing*: We developed approaches and protocols for using remote sensing to map land and lake cover on a statewide basis for Wisconsin (Bolstad and Lillesand 1992a,b,c, Lillesand 1993a,b, Benson and MacKenzie 1995) as well as ice-off dates for wide regions (Wynne and Lillesand 1993, Wynne et al. 1996).

Human-Lake Interactions

- *Nutrient Load Modelling*: A model to predict annual phosphorus loads to Lake Mendota from land use in the watershed has been developed, validated, and used to explore the consequences of progressive urbanization (Soranno et al. 1996). P input rates were compared in detail with internal recycling rates (Soranno 1995). A model to predict the frequency distribution of P loading events from land use and precipitation data is partially completed (Figure 8). This model will be used to explore scenarios of climate change interacting with land-use change (research area 5, below).

Cross Disciplinary Collaboration

Our roots are in limnology which is traditionally interdisciplinary across the natural sciences, i.e., physics, chemistry, and biology. Our analyses link processes across these disciplines (research area 1 - 5, below). We are an interactive group working at and among levels of ecological organization from autecology to landscape ecology. We study trophic ecology, biogeochemistry, population biology, determinants of biodiversity, landscape ecology, and mixes of these. We use multiple approaches including modeling, experimentation, description, and comparative ecology. We began incorporating social sciences with the 1994 augmentation. A highly successful cross disciplinary workshop was held in November 1994 and was followed by a seminar in Fall 1995 entitled *Lakes and Society* led by a limnologist and a rural sociologist. Our present proposal has a strong human component (research area 5).

We initiate and participate in research projects and the network data management process at an intersite level. We organized an intersite analysis of variability of North American Ecosystems that included data from 12 LTER sites (Magnuson et al. 1991, Kratz et al. 1995). Regardless of biome, spatial variability was greater than interyear variability and plant or animal parameters were more variable in space and time than chemical or physical variables (Figure 9). We expanded this approach to compare spatial heterogeneity at the scale of full-LANDSAT scenes for 14 scenes that include LTER sites (Riera et al. in prep.) (Figure 10).

Other Interactions and Education

Our LTER site has been successful in catalyzing LTER-related research by others as well as by our own researchers. The potential for interacting with LTER researchers and our databases has been key in generating this interest. These other projects are funded from a range of federal (NSF, EPA, DOE, USGS, USDA-SCS, NASA), state (Wisconsin DNR, University of Wisconsin) and private (endowments, Pew, and EPRI) sources. From 1990-1995 an average of $1,624,000 per year of additional research has been associated with the LTER site; of this an average of $279,000 per year is from other NSF funding and $1,324,000 is from non-NSF sources. During the same six years our LTER base plus the 1994 augmentation and other supplements (GIS, Technical, REU) averaged $653,000.

We have contributed significantly to education, 16 MS and 8 Ph.D. theses related to LTER research were produced over the six years. Education of undergraduates and outreach are covered in Section 6: Outreach. Internationally, we have hosted visiting investigators, and post-doctoral, and graduate students, including long-term collaborations with researchers from Germany, China, Spain, Scotland, Honduras, and Venezuela and shorter-term visits from Hungarian, Czechoslovakian, and Russian scientists.

Section 3. Proposed Research

Conceptual Framework

Lakes are conspicuous, valuable and vulnerable landscape features throughout the world. Small, inland lakes are particularly prominent throughout the Upper Great Lakes region of North America. From the fertile, loess-capped soils of the north-central U.S. to the Precambrian outcrops of the Canadian Shield, the thousands of inland lakes play a central role in regional hydrologic and biogeochemical cycles, in biological processes influencing the area's diversity of aquatic and terrestrial life, and in a wide range of human activities. Over the past two centuries, deforestation, fire suppression, agriculture, industrialization, and urbanization have transformed landscapes within the region and fundamentally altered the relationships of lakes to their surroundings. Patterns of change in lakes and surrounding landscapes have been influenced by the availability of lakes for irrigation, industry, human waste, transportation, fishing, and recreation. For the next century and beyond, the quality of life and the economies of the region will depend upon the quality of the lakes.

Our research approach considers lakes as interactive components of their environment. As collectors of water, energy, solutes, and pollutants from the landscape and atmosphere, as habitats for aquatic biota, and as attractors of human activities, lakes affect and are affected by natural and human-induced changes in the local and regional landscape and atmosphere. The North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program seeks to understand the long-term ecology of lakes and their interactions with a range of important landscape, atmospheric, and human processes. We use a nested set of spatial scales including individual lakes, multiple neighboring lakes, entire lake districts, and the Upper Great Lakes region (Figure 11). This multiscale approach distinguishes our efforts from most previous limnological research and provides an opportunity to identify controlling factors operating at scales ranging from individual lakes to regions. Within this conceptual framework, our program has the following five interrelated goals.

(1) Perceive long-term changes in the physical, chemical, and biological properties of lake ecosystems.

This goal includes the collection and management of our core datasets. Most of the research we describe depends on these continually evolving, long-term datasets. We propose to add two new long-term core datasets; one on coarse woody debris, an important structural feature of the littoral zone of lakes, the other on stable isotopes of hydrogen and oxygen, important hydrologic tracers.

(2) Understand interactions among physical, chemical, and biological processes within lakes and their influences on lake characteristics and long-term dynamics.

This goal is focused on the within-lake scale. We will examine such processes as the interaction of nutrient and food-web effects on phytoplankton; the influence of bacterial processes on nutrient availability and phytoplankton growth; the effects of lake chemistry, morphometry and foodweb structure on the fate of nutrients; the influence of functional compensation among species on ecosystem resilience to environmental change; and the way exotic species affect lakes.

(3) Develop a regional understanding of lake ecosystems through an analysis of the patterns and processes organizing lake districts.

Here, we address patterns and processes important at lake-district to regional scales. We propose to extend analyses performed previously on a subset of lakes in northern Wisconsin to the entire lake-district, and assess the generality of our results using comparisons with patterns observed at other lake districts within the region. We propose to examine the degree to which lakes exhibit synchronous dynamics, the role spatial positioning of lakes plays in controlling lake attributes and dynamics, and how patterns of connectivity among lakes can be important to regional biodiversity.

(4) Develop a regional understanding of lake ecosystems through integration of atmospheric, hydrologic and biotic processes.

This goal takes a process-modeling approach to understanding atmospheric, terrestrial, hydrologic, and aquatic linkages at lake-district to regional scales. We propose linking several process models to allow spatially-explicit tracking of water movement through the hydrosphere. We ask how changes in climate affect lakes both directly by altering lake thermal dynamics, and indirectly through changes in hydrologic processes in the terrestrial environment.

(5) Understand the way human, hydrologic, and biogeochemical processes interact within the terrestrial landscape to affect lakes and the way lakes, in turn, influence these interactions.

In this final goal, we focus on the feedback loop between terrestrial processes and lake processes. Lakes are affected directly by landscape processes, but also participate in feedbacks that alter these processes, largely through changes in human perceptions and actions. We focus on interdisciplinary analyses of land-use change and lake response.

In addressing these five goals we use a variety of approaches including long-term observations, small- and large-scale experiments, comparative studies, and process modeling. In the sections that follow, we elaborate on each of these five goals.

(1) Perceive long-term changes in the physical, chemical, and biological properties of lake ecosystems.

Rationale. One of the basic goals of the North Temperate Lake LTER program is and has been the collection and management of ecologically important data that allow investigators to observe and analyze long-term changes in physical, chemical, and biological features of lakes. Long-term observations and analyses are crucial to understanding lake ecology. Natural phenomena, such as strong year-classes of long-lived predators or a series of drought years, can cause multi-year to decadal effects in lakes, often with substantial time lags between cause and effect (Magnuson et al. 1990, Carpenter and Leavitt 1991). In addition, many human-induced pressures influencing lakes, such as invasions of exotic species, eutrophication, and climate change, operate over time scales of years to decades or longer. Holling (1995) points out that the accumulation of these effects can cause changes which are difficult to understand without a long-term context. To provide such a context for our research, we collect and maintain a series of 'core' databases (Table 1, Table 3). These datasets provide the basis for addressing most of our research questions.

Background. Over the past 15 years we have designed and implemented a balanced and integrated data collection program (Kratz et al. 1986, Magnuson and Bowser 1990). Our choices of lakes and measurements have been guided by a desire to address important interdisciplinary questions regarding the ecology and management of lakes from a long-term perspective at individual lake, multiple lake, lake-district and regional scales.

We focused our data collection on two sets of lakes and their surrounding landscapes. One set is in the forested and tourism-dominated Northern Highland Lake District in northern Wisconsin, the other is in the agricultural- and urban-dominated landscape in and near Madison in southern Wisconsin (Figure 12). Both regions have a substantial history of limnological research dating back to 1900 (Frey 1963).

In addition, we have working relationships with two Canadian groups with similar data on two other lake districts, the Experimental Lakes Area in western Ontario and the Dorset Research Centre in eastern Ontario (see Section 4: Project Management). Collectively, the data and research programs at these four focal lake districts afford a unique opportunity for regional analyses.

In northern Wisconsin, beginning in 1981, we focused on a suite of lakes and surrounding terrestrial areas linked through a common groundwater and surface water flow system and sharing a common climatic, edaphic, and biogeographic regime. The lake set includes oligotrophic, dystrophic, and mesotrophic lakes (Table 4, Figure 12). Our seven primary study lakes, located within 5 km of the Trout Lake Station, were chosen to represent marked differences in size, morphometry and habitat diversity, in thermal and chemical features, in species richness and assemblies, and in position in the groundwater flow system. In addition to the seven primary lakes we also have a set of secondary lakes for which less complete information is collected. The choice of secondary lakes and types of measurements change over time. These lakes are used for comparisons with primary lakes on specific research questions.

With the augmentation of our LTER project in November 1994, we added four primary study lakes in southern Wisconsin (Table 4). These four eutrophic lakes were chosen in a 2x2 design of urban vs agricultural setting and headwater vs lower in the landscape. Substantial historical data are available on these lakes. Lake Mendota has been studied since 1888 (Kitchell 1992, Brock 1985) and had been an LTER secondary lake prior to the 1994 augmentation. The Wisconsin DNR has maintained a high-quality database for Lakes Mendota and Monona since 1976 (Lathrop et al. 1992, Lathrop and Carpenter 1992a,b) which is now being integrated with the NTL-LTER database. Lake Wingra was studied intensively during the IBP program in the early 1970's (Watson and Loucks 1979). Fish Lake is part of a Wisconsin DNR network of sentinel lakes. WDNR and the Center for Limnology have studied Lakes Fish and Wingra since 1991 through a collaborative project on macrophyte-fish interactions (Trebitz et al. 1993, Carpenter et al. 1995a).

Our sampling program allows comparisons of parameters and processes among seasons, years, lakes, and lake districts. We sample most major physical, chemical and biological parameters (Table 3) with sampling frequencies tuned to the dynamics of individual parameters. We sample most intensively at four key times of the year: spring overturn, maximum stratification in summer, fall overturn, and winter stratification. Chemically these periods are important because differences between spring and fall overturns indicate a net gain or removal of chemical species from the water column. At periods of maximum stratification, conditions are most different from mixis, and depletion of epilimnetic nutrients and hypolimnetic oxygen can severely stress or limit biological components. Complete cation-anion balances are computed for each period. Nutrients, pH, inorganic and organic carbon are sampled every two or four weeks, depending on the lake and the nutrient. Temperature, dissolved oxygen, chlorophyll a, light penetration, and zooplankton abundance are measured every two weeks during the open-water season and every five weeks under ice cover. Samples for phytoplankton community composition are collected and primary production rates are measured every two weeks from selected lakes. Parameters that vary over longer time scales are measured annually in August. These include macrophyte distribution, fishes (abundance, biomass, and community structure), and benthic invertebrate abundance. Groundwater levels in selected wells are measured monthly and groundwater chemistry from a subset of these wells is measured annually. In addition, we maintain an automated land-based weather station at the local airport 10 km from Trout Lake; a raft on Sparkling Lake for measurements of evaporation, wind stress, and high resolution thermal structure; and have access to National Weather Service data from the Madison airport.

In addition to providing comprehensive limnological data, this sampling program positions us to detect invading exotic species in our primary lakes. Potential new invaders include many European species (Mills et al. 1993) that have reached the Laurentian Great Lakes. These large lakes now act as a nearby source (mainland in an island biogeographic sense) of colonists including fishes (ruffe, rainbow smelt, rudd, round goby, etc.), zooplankton (*Bythotrephes cederstroemi*, *Eurytemora affinis*, etc.), molluscs (zebra mussels, fingernail clams, and a variety of snails), and a macrophyte (Eurasian watermilfoil, which occupies the Madison area lakes and could invade the Trout Lake area (Nichols and Lathrop 1994, Nichols and Yandell 1995)). We have designed our sampling so that introductions of these or other invading species will be discovered early and we can implement specific research activities to understand consequences of these introductions.

To provide basic information about the terrestrial landscapes surrounding our study lakes, we have developed a geographic information system that includes data layers on land cover (from presettlement to present), soils, roads, and geological substrate. We have acquired multiple Landsat Thematic Mapper and SPOT scenes for both the Trout Lake and Madison areas (Table 3). Members of the LTER research group have been leaders in the research and development of the Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data (WISCLAND), a statewide land-cover mapping program cooperatively sponsored by federal, state, and local agencies. When fully implemented WISCLAND will provide statewide land cover mapping for Wisconsin at 30 meter resolution. WISCLAND incorporates numerous state-of-the-art image processing procedures to ensure accuracy and categorical detail of the classification. These procedures include: dual date TM data to use phenology to aid vegetation classification; an ecoregion-by-ecoregion study area stratification; separate classifications of rural vs. urban areas and wetlands vs. uplands; applications of hybrid "guided" clustering and maximum likelihood classification; and employment of stratified, systematic, non-aligned statistically-based sampling for collection of training and accuracy assessment data. With over 40,000 field verified sample polygons distributed across all of Wisconsin, WISCLAND is one of the largest and most technologically complex land cover mapping programs in the world. The WISCLAND land cover classification system and image processing protocol have been adopted for use throughout Minnesota and Michigan as part of the Upper Midwest GAP Analysis Program (Lillesand 1996). NTL is ideally positioned in the center of the regional land cover database resulting from these efforts.

***Proposed New Core Datasets*.** Collecting and maintaining the core datasets listed in Table 3 provide the basis for addressing the research questions presented in this proposal. We will continue to collect and maintain these datasets. In addition we will add two new datasets, one on coarse woody debris, the other on stable isotopes of oxygen and hydrogen in lakes, groundwaters, and precipitation.

Coarse woody debris (CWD) provides habitat and is a critical ecosystem component in streams and rivers (Harmon et al. 1986, Andrus et al. 1988, Bilby and Ward 1991), but its role in lake ecology is poorly understood. In lakes, CWD is likely to be important as habitat for periphyton, invertebrates, and fish. In lakes, as in rivers, human activities significantly alter CWD inputs and standing stocks (Spies et al. 1988, Maser and Sedell 1994). For example, cottage development is associated with a dramatic reduction in CWD (Christensen et al. 1996). Depletion of CWD could affect lakes for centuries (Andrus et al. 1988, Maser and Sedell 1994). Yet the dynamics of CWD in lakes is unknown. We will initiate a program to document rates of introduction and removal of CWD in littoral zones with different amounts of cottage development and contrasting structure of riparian forests. CWD in each primary NTL-LTER study lake will be mapped annually to ca. 1 meter accuracy using a global positioning system. We will be able to estimate annual input and removal rates as a function of cottage density, shoreline use, and riparian vegetation. The database will also provide a long-term context for graduate student and REU research projects to study influences of CWD by periphyton, invertebrates and fishes.

Measurement of stable isotopes will allow us to document variation in the annual fluxes of water to lakes through groundwater and direct precipitation, key links to external fluxes of nutrient and major ions to lakes. Krabbenhoft et al. (1990b) and Gat et al. (1994) have emphasized the use of stable isotopes of oxygen and hydrogen to quantify hydrologic budgets of seepage lakes and the dominant role of groundwater in the flux of major ions and nutrients to lakes. We will sample stable isotopes quarterly in LTER lakes and local precipitation and calculate year to year variation in groundwater fluxes to lakes. Combined with core groundwater chemical data, annual fluxes of nutrients and other solutes to lakes and their interannual variation will be estimated. Results will provide a valuable link between external and internal controls on in-lake processes.

(2) Understand interactions among physical, chemical, and biological processes within lakes and their influences on lake characteristics and long-term dynamics.

***Rationale and Background*.** Understanding the fundamental processes operating within lakes is a focus of the NTL-LTER program. Internal physical, chemical, and biological processes filter the effects of external factors on the long-term properties of lake ecosystems (e.g., Reynolds 1984, Likens 1985, Carpenter 1988). Evaluations of external factors (research areas 4 and 5) controlling broader-scale patterns in the properties of lakes within a landscape (research area 3) draw on a substantial knowledge of mechanisms controlling the properties of individual lakes.

Our past work on key linkages between in-lake processes and lake-ecosystem features helped us identify five research questions. These efforts, ranging from intensive experimental and observational studies on single lakes to multi-lake comparisons, center on processes occurring within lakes. A challenge in ecology is to evaluate interactions among patterns and processes that fluctuate at different time scales (O'Neill et al. 1986; Carpenter 1988, Holling 1995). Our diverse approaches combining mechanism with context help clarify linkages among phenomena that span a wide range of spatial and temporal scales.

Proposed Research.

a) How do nutrient availability and food-web structure interact in lakes of differing trophic status to influence phytoplankton dynamics?

Phytoplankton biomass in lakes can be controlled by nutrients and food-web processes, but the interactions of these factors are not yet predictable (Reynolds 1994). Abundant evidence links phosphorus inputs to primary production (Schindler 1977, 1978). Food-web processes can affect phytoplankton through grazing (Hrbacek et al. 1961, Gulati et al. 1990, Carpenter and Kitchell 1993) or recycling of nutrients (Carpenter et al. 1992, Elser and Hassett 1994). However, food-web manipulations of lakes yield variable results (Reynolds 1994). We expect that a lake's response to shifts in nutrients or food-web processes will depend on its trophic condition.

We will examine the role of trophic condition by comparing nutrient and food web effects on phytoplankton in lakes of contrasting trophic state. We have observed substantial inter-annual changes in the water clarity of eutrophic Lake Mendota and oligotrophic Crystal Lake (Figure 13). In both lakes, shifts in the abundance of a dominant planktivorous fish (yellow perch in Crystal, cisco in Mendota) correlate with changes in water clarity (Magnuson 1990; Rudstam et al. 1993, Johnson 1995, Lathrop et al. 1996). We hypothesize that both nutrient and food-web dynamics drive year-to-year changes in water clarity, but that the mechanisms by which these processes influence producers differ. Specifically, we predict that, in the oligotrophic system, nutrient effects are mediated by grazers' excretions, whereas, in the eutrophic system, phytoplankton are controlled by an interaction of grazing and nutrient loading from runoff and hypolimnetic entrainment.

Long-term data will be combined with rate estimates from the literature and short-term experiments (e.g. Lehman and Sandgren 1985, Elser and Goldman 1991, Elser and Hassett 1994), to assess the relative impacts of grazing, nutrient recycling by grazers, and phosphorus loading on changes in phytoplankton abundance. Necessary data on nutrients, zooplankton, and phytoplankton are in hand. Time-series methods (Box et al. 1994) will be used to estimate the effects of changes in nutrients and grazers on phytoplankton using long-term data.

While grazer effects on phytoplankton have been measured in lakes across a range of phosphorus levels (Jeppesen et al. 1990, Reynolds 1994, Carpenter et al. 1996), the general role of trophic status is still not clear. In our study, the context provided by a long-term perspective and strongly contrasting lakes will provide insight into the role of trophic conditions on the interaction of zooplankton, nutrients and phytoplankton. A replacement of yellow perch in

Crystal Lake by invading rainbow smelt (Question e, below) provides an additional set of conditions within which nutrient/food-web interactions can be evaluated.

b) How does the bacterial community influence nutrient availability and phytoplankton growth?

Bacteria may have both positive and negative effects on the availability of nutrients to phytoplankton through remineralization and uptake. In some situations, bacterial growth appears to be phosphorus limited (Morris and Lewis 1992, Coveney and Wetzel 1995). At the same time, bacterial growth may also be influenced by organics released by algae (Cole et al. 1988). Predicting phytoplankton-bacteria interactions is complex. We will measure seasonal and intra-lake differences in growth limitation of bacteria and phytoplankton to determine the nature of their interactions for resources.

Mesocosm experiments will be used to determine nutrient limitation of bacterial and algal growth by carbon, nitrogen, and phosphorus. A dilution method, similar to that of Morris and Lewis (1992), will be used to minimize the influence of grazers in nutrient limitation experiments. We will test bacterial influences on algal growth using bacterial growth inhibitors and bacterial additions in short-term experiments. All experiments will be conducted across NTL lakes of contrasting trophic status, and during different seasons, to determine hydrologic, geologic and seasonal influences.

We predict that the influence of bacteria on algal growth will decrease during periods when each group is limited by a different nutrient. Limiting nutrients are expected to change between lakes and seasons as indicated by different ratios of available nutrients (Le et al. 1994). We predict that bacteria will compete for phosphorus and limit algal growth in the oligotrophic, phosphorus-poor lakes of the Trout Lake region. We anticipate that bacterial growth is more likely to be limited by carbon, and algal growth by phosphorus and/or nitrogen in the nutrient-rich southern Wisconsin lakes. Bacteria should influence algal growth less in these eutrophic lakes. Because bacterial growth can be strongly temperature limited in cold waters (White et al. 1991, Shiah and Ducklow 1994), we expect bacteria to influence algal growth less during spring and fall.

Understanding the relationship between nutrient availability and algal growth is central to lake management. Our study will demarcate the conditions under which bacteria influence the availability of nutrients to phytoplankton. Knowledge of intra-lake and seasonal differences in bacterial-algal interactions will increase our understanding of how phytoplankton dynamics in lake ecosystems are controlled.

c) How do chemistry, morphometry and food-web structure of lakes interact to influence the availability of spring nutrients to summer communities?

Spring is a critical time when weather and a lake's community structure can affect nutrient availability during later seasons. A combination of increasing insolation, high nutrient concentrations and low herbivory often lead to a spring build up of phytoplankton biomass (Sommer et al. 1986). The fraction of this biomass that sinks out of recycling zones helps determine total annual production (Reynolds 1984; Harris 1986, Guy et al. 1994, Poister et al. 1994).

We propose that chemistry, morphometry and food-web structure determine the fraction of spring P that becomes unavailable for later use. Si:P ratios and morphometry are related to net total phosphorus (TP) dynamics in NTL-LTER lakes. We will make use of strong gradients in Si, P, and morphometry among the lakes near Trout Lake and Madison to test four predictions. 1) Lakes with high initial Si:TP ratios will lose more of their spring TP to sinking because diatoms will dominate their spring phytoplankton communities. 2) Among lakes with low Si:P, larger populations of crustacean zooplankton will be associated with greater losses of spring P. 3) Lakes with littoral zones that are large relative to their mixed-layer volumes will retain more P within the water column. 4) Interannual variability in the ratio of spring TP: summer TP will be greatest in larger lakes where the depth and timing of stratification varies most from year to year. Our work will draw upon previous NTL-LTER studies linking lake-silica dynamics with ground-water inputs (Hurley et al. 1985, Krabbenhoft 1988) and tying patterns of ecosystem variability to landscape position (Kratz et al. 1991b). We will compare sinking fluxes and their standard deviations measured by inverse modeling (Jackson and Matsu'ura 1985, Vezina 1989, Vezina and Pace 1994).

Comparative studies of flow networks have proven powerful in marine ecology (Wulff et al. 1989), stream ecology (DeAngelis et al. 1989), and community ecology (Pimm 1991, DeAngelis 1992). Our inverse modeling is the basis for a comparable synthetic approach to P cycles of diverse lakes.

d) What is the role of functional compensation in ecosystem resilience to environmental change?

Ecological responses to stress typically involve dramatic changes at the population level, but major disruptions in ecosystem processes are less frequent (Schindler 1987, Schindler et al. 1991, Frost et al. 1995, Tilman in press). Previous studies suggest that compensatory dynamics among functionally-similar species play a major role in determining ecosystem resilience to stress; however, this phenomenon is poorly understood (Ives 1995, Frost et al. 1992, Lawton and Brown 1993, Walker 1995). Understanding the factors that determine functional compensation in the dynamics of stressed communities will be critical to predicting ecological responses in a changing environment. We propose to investigate the interplay between functional compensation and ecosystem resilience in unperturbed and manipulated lakes.

Using the NTL-LTER zooplankton dataset, we have begun to assess the responses of individual species and groups of species in the same trophic guild to naturally-occurring environmental fluctuations. Preliminary results indicate that the summed biomass of species in the same trophic guild is less variable than biomass of individual species, suggesting that functional compensation is prevalent in the dynamics of zooplankton communities (Carpenter et al. 1993). To investigate links between diversity and community-level stability, we plan to compare the degree of functional compensation among lakes with a gradient of zooplankton species richness. We will use known allometric relationships to explore the implications of compensatory changes in zooplankton community structure for grazing potential. To assess the relationship between functional compensation and resilience in stressed systems, we will build upon our past experience and compare responses of different plankton assemblages to acidification in replicated mesocosms.

Our study of functional compensation in ecosystem response to environmental change has important implications for understanding ecological resilience, designing monitoring programs, and planning for conservation. Resilience is a core concept in ecology and ecosystem management, yet its underlying mechanisms remain poorly understood (Pimm 1991, DeAngelis et al. 1989, Gunderson et al. 1995). Ideal environmental indicators foreshadow any loss of ecosystem resilience (Gunderson et al. 1995). Conservation planning is increasingly moving toward an integration of population, community, and ecosystem processes (Franklin 1994, Jones and Lawton 1995); that will require explicit consideration of functional compensation.

e) What controls the effects of exotic-species invasions on lake-ecosystems?

Invasions by exotic organisms can lead to a variety of fundamental changes in lake ecosystems (Paine and Zaret 1975, Moyle 1986, Kaufman 1992, Lodge 1993a,b, Mills et al. 1993). Despite the recent high frequency of such invasions, their effects remain difficult to predict (Drake et al. 1989). We propose evaluating the effects on lake ecosystems of the rainbow smelt (which has already invaded two of our lakes) and determining the mechanisms that prompt the changes. The rainbow smelt, native to Atlantic coastal areas of North America, is spreading throughout inland lakes in the upper Great Lakes region and has invaded Crystal and Sparkling Lakes. In Crystal Lake the invasion has led to declines in the lake's historically dominant planktivore, yellow perch, through resource competition (Hrabik 1995). Year-to-year fluctuations in yellow perch abundance had previously had substantial effects on Crystal Lake's water clarity (see research area 2a above). Invasion-generated shifts in the abundance of zooplanktivorous fishes can lead to fundamental changes in a lake's food-web (e.g., Brooks and Dodson 1965, Wells 1970). Such shifts generate effects that cascade down to lower trophic levels, ultimately altering ecosystem dynamics (Vanni et al. 1991, Luecke et al. 1992, Rudstam et al. 1993, Carpenter and Kitchell 1993, Helminen and Sarvala 1994). Using our long-term core databases (see research area 1, above) we will assess the impact the shift from yellow perch to rainbow smelt in Crystal Lake will have on food-web interactions.

Changes in Crystal Lake are likely to occur through two mechanisms. Smelt prefer smaller zooplankton prey (Hrabik 1995) and cooler temperatures than perch. They can also maintain higher consumption rates at cooler temperatures and over a longer growing season. We will test the importance of these mechanisms using small-scale experiments. We predict shifts in zooplankton community structure, abundance, and vertical distribution. By coordinating this study with analyses of plankton and water clarity change (Question a, above), we will assess effects of smelt invasions at the ecosystem level.

(3) Develop a regional understanding of lake ecosystems through an analysis of the patterns and processes organizing lake districts

Rationale and Background. Lakes in a lake district share a common climatic regime and geologic setting, but can differ markedly in physical, chemical, and biological attributes, as well as in their responses to regional phenomena such as climatic events, deposition of atmospheric pollutants, invasion by exotic species, or landscape alteration (Eilers et al. 1983, Cook and Jager 1991, Kratz et al. 1991b, Webster et al. 1996). Here we describe our efforts to develop a general conceptual framework which explains the spatial variability in properties of lakes at multiple lake, lake district and regional scales. We expect over the next six years that this research will lead to a new and powerful integration of lake-landscape interactions, prompting new ideas that we will develop and test. This framework will be analogous in scope and power to the River Continuum Concept for flowing waters (Vannote et al. 1980, Johnson et al. 1995).

We have accumulated substantial evidence for organizing patterns and processes at landscape scales within the Northern Highland Lake District. Diverse attributes, including lake area, major ion chemistry, vertical distribution of primary production, benthic trophic interactions, and species richness of fishes, have all been linked with the spatial position of lakes within local and regional hydrologic flow systems (Eilers et al. 1983, Webster et al. 1996, Kratz et al. 1991b, Kratz et al. in review, Riera et al. in prep) (Figure 14, Figure 15).

The generality of these organizing patterns and processes will be tested by extending this landscape framework from the Northern Highland to the Experimental Lakes Area, Dorset, and Madison lake districts (Figure 11). The four lake districts represent broad regional gradients, contrasting drivers of lake variability, and histories of disturbance. Most importantly, all four lake districts are sites of extensive research programs of unusual longevity. Comparisons across these four focal lake districts will be developed in two ways. First, we can compare the lake districts and test for generality of results observed at any one of them. Second, we can pool data from all lake districts to gain a regional perspective across the major ecoregions of the Upper Great Lakes region.

We expect that the relative importance of organizing factors changes as a function of spatial scale. Addressing these scale dependencies is an important goal of our proposed research.

Proposed Research. The history of research at each of the four lake districts provides us with a unique opportunity to understand patterns and processes organizing lake districts. We have identified three areas for emphasis during the next six years.

a. At what spatial and temporal scales, for which types of limnological variables, and to what extent do lakes vary synchronously?

Lakes are affected by many driving variables acting at a variety of scales. We expect the composite behavior of lakes over a large region to reflect a complex mixture of local, intermediate, and regionwide drivers. The scale at which a particular driving force is most important can be predicted by analyzing the temporal and spatial scales at which related limnological variables exhibit coherency (synchronous temporal variability, Magnuson et al. 1990). For example, if temperature and rainfall are important regional drivers on an annual time scale, we would expect lake water levels to increase regionwide in wet years, and decrease in dry years. However, at weekly scales, lakes levels may show little coherence across the entire region but high coherence within the same local drainage system.

We will use data from the four lake districts to test for coherency in a diverse set of physical, chemical, and biological variables at local, lake district, and regional spatial scales, and at a variety of time scales. We have begun these analyses for selected physical parameters in the entire Upper Great Lakes Region, and have found a high degree of coherence in lake water temperature (Benson et al. in prep). We will expand this research to the full set of physical, chemical, and biological lake attributes.

We plan to assess the generality of results from individual districts by comparing patterns of coherency among lake districts. In the Northern Highland Lake District, lakes tend to be more coherent in physical parameters, less so in chemical parameters, and least in biological parameters (Magnuson et al. 1990). This pattern may not be repeated in other lake districts; important differences may emerge in the analysis of other lake districts. For example, we expect that phosphorus loading, which shows no among-year coherence in the northern Wisconsin lakes, will be coherent in southern Wisconsin because agricultural runoff accounts for the major phosphorus input to these southern Wisconsin lakes, but is not an important driver in the north.

b. How does a lake's spatial position influence its physical, chemical, and biological properties?

A focal point for research at our site has been the development of a relationship between a lake's spatial position in the landscape and its physical, chemical, and biological properties (Magnuson et al. 1990, Kratz et al. 1991b, Krabbenhoft et al. 1994, Kratz et al. 1995, Webster et al. 1996). There are four logical extensions of this work that we propose to pursue.

First, we need to refine a simple quantitative method to locate or categorize the position of lakes in the hydrologic flow system. In lake districts dominated by surface water connections, lake order can be defined easily using criteria similar to those used to classify streams. However, in the Northern Highland Lake District, many lakes have no surface water inlets or outlets and groundwater provides the hydrologic connection between lakes. For these lakes we can quantify relative position in the landscape by estimating the percentage of the lake's hydrologic budget that comes from groundwater inputs using stable isotopes of hydrogen and oxygen as tracers (Krabbenhoft et al. 1990a,b, 1994). We will pursue linking surface- and groundwater- based definitions of lake order to develop a general quantification of landscape position that is inclusive of both seepage and drainage lakes.

Second, we propose extending our ordering of lake attributes according to position in the hydrologic flow system from the seven primary LTER lakes in northern Wisconsin to the entire Northern Highland Lake District. Although multiple historic and recent surveys of lake characteristics in the district provide a rich collection of limnological information (Juday et al. 1938, Black et al. 1963, Eilers et al. 1983, Linthurst et al. 1986, Tonn et al. 1990), these data have never been analyzed in a spatially explicit context. Initially, we will use GIS to assess relationships between a lake's landscape position and limnological parameters such as lake area, specific conductance, dissolved organic carbon, and fish species richness. Later we expect to expand this analysis to other parameters.

Remote sensing technology will allow us to characterize the absorption and scattering properties of constituents such as chlorophyll, DOC, and suspended solids in lakes throughout a lake district. We propose to measure wavelength-specific absorption coefficients (e.g., Bolgrien et al. 1995) using spectrophotometric and radiometric data, mixture decomposition methods, and our core lake data. The removal of atmospheric effects from radiometric data, critical to bio-optical modeling, will be facilitated by our participation in the NASA/LTER sun photometer network. We hypothesize that coefficients will be related to phytoplankton community structure and landscape variables regulating allochthonous inputs. Our ultimate objective is to develop a bio-optical model for constituent concentrations (Bukata et al. 1995) enabling remote monitoring of changes in regional lake water quality.

Third, we plan to extend our conceptual framework of lake-landscape position, which was developed in a lake district structured primarily by groundwater input, to the two lake districts on the Canadian Shield, both of which are dominated by surface water flow. We will start by using this framework to analyze the response of lakes in each of the lake districts to the regionwide drought of the late 1980's. We will test the hypothesis that the response of lakes to drought depends on landscape position and water retention time. For the first time, we are in a position to comprehensively analyze lake response to regional climatic events such as drought in a landscape context.

Finally, we propose to examine spatial scale dependencies of landscape effects on the chemistry of north temperate lakes. Lake chemistry can often be predicted by characteristics of the surrounding landscape, but the spatial scales at which landscape attributes exert a detectable influence on lakes are not well understood. We will start by asking two questions. First, what attributes of the terrestrial landscape explain significant variability in chemistry among lakes, and at what spatial scales are these effects apparent? And, second, does the spatial scale of influence vary between seepage lakes, which lack surface water inlets and outlets, and drainage lakes? We will approach these questions by analyzing the relationship between lake chemistry and landscape parameters (e.g., area of watershed in peatlands, vegetation and slope of the surrounding watershed) within buffer zones of increasing width for approximately 100 lakes. After an analysis of patterns in the Northern Highland Lake District, we will expand our analysis to include lakes from the other lake districts. We expect that the spatial scale of landscape influence will be a function of lake type (seepage vs drainage), hydrologic regime (atmospheric-dominated, groundwater-dominated, or surface-water dominated) and geologic setting.

Collectively, we expect results from these four objectives will enable us to derive a conceptual framework relating lake spatial position to static physical, biological, and chemical attributes as well as the dynamic responses of small inland lakes to regional phenomena in the Upper Great Lakes region.

c. How does spatial connectivity of lakes in a region influence the relation between long-term local and regional diversity?

Communities are assembled through a variety of processes that occur over a wide range of spatial and temporal scales, including both within-lake and regional processes (Ricklefs 1987, Ricklefs and Schluter 1993). The extent of connectivity among habitats will influence the relative effects of regional processes on species composition (Figure 16). Island biogeography theory and related concepts provide an appropriate framework for evaluating connectivity within a lake district (Barbour and Brown 1974, Magnuson 1976). Studies of fish diversity in northern Wisconsin, Finland and Alberta show that both local extinction factors and regional colonization factors are important determinants (Tonn et al. 1990, Magnuson et al. MS). High estimates of species turnover for zooplankton (Arnott et al. MS) and fishes (Magnuson et al. 1994) and low inter-annual variation in species richness suggests that a balance exists between colonization and extinction processes. The importance of colonization will depend on interactions between the form and extent of connectivity and the vagility of the taxa. Within lake districts, avenues of connectivity include animal transport (including humans), streams, and wind and storm events. Plankton, fishes, and snails differ in vagility and utilize different dispersal modes. We propose to investigate the relation between lake connectivity, species vagility and species diversity in several north temperate lake districts.

By characterizing how connectivity and species vagility interact, we can assess how system openness influences long-term local and regional diversity. For zooplankton, our regional assessment of diversity will be extended to a continental scale using an extensive spatial database (Dodson 1992). In regions with isolated lakes and for species with low vagility, we expect long-term local diversity to be low relative to long-term regional diversity. With a highly connected lake district and vagil species, long-term local diversity should approximate the long-term regional diversity. We expect that with less vagil species in highly connected systems, the relation between long-term local diversity and long-term regional diversity will be affected by the taxa's dispersal mechanisms and the manner in which the system is connected.

Biodiversity studies are limited by taxonomic knowledge and resolution. Species composition may change owing to taxonomic effort and revision, rather than actual changes in community composition. We will quantify effects of taxonomic shifts by re-evaluating the taxonomy of species from archived samples.

One measure of connectivity may be the dispersion patterns of exotic species; several exotics are spreading into Wisconsin lakes. Distribution patterns and rates of colonization to new water bodies may indicate the extent of connectivity among lakes. We will reconstruct colonization patterns of exotic species (such as rainbow smelt, Eurasian watermilfoil, and rusty crayfish) to determine how lake connectivity influences the species movement through lake districts.

We will develop a spatially explicit dispersal model to generate time scenarios for distribution patterns via alternate dispersal vectors. We will do this for dispersal from those lakes first known to contain smelt and rusty crayfish in the Northern Highlands Lake District and compare that with present distributions. Future scenarios will be made for comparisons later in the long term. Considering the island nature of the lake district, the process is expected to play out over decades and centuries. These analyses will help guide natural resource agencies to interfere with dispersal where possible, and where not, to prepare for the inevitable. The later alternative will be guided, in part, from our inlake studies of the effects of invaders on lakes (research question 2c).

(4) Develop a regional understanding of lake ecosystems by integrating atmospheric, hydrologic, and terrestrial ecosystem processes.

***Rationale and Background*.** Atmospheric and terrestrial ecosystem processes are important in determining the amount and chemical properties of water in aquatic ecosystems. We plan to examine key linkages between the atmosphere, terrestrial ecosystems, and aquatic systems for small inland lakes in the Great Lakes region. Of particular interest are mechanisms controlling how these interacting systems respond to variations in climate and changes in land cover. Specifically, we will extend our understanding of linkages between atmospheric, aquatic, and terrestrial ecosystems to the regional scale by using a combination of process-based modeling and on site and remote sensing databases.

***Proposed Research*.**

a. How do variations in climate affect lakes?

Regional-scale variations in climate manifest themselves in many ecological phenomena, including changes in lake thermodynamics and biology. We propose new modeling and comparative studies to analyze linkages of climate and lakes at regional scales.

To study changes in lakes resulting from climate variability, we simulate lake thermodynamics with a recent version of the Dynamic Reservoir Simulation Model (DYRESM) of Imberger and Patterson (1981). Seasonal thermal structures are significant for vertical distribution of organisms (Magnuson and DeStasio 1996) and chemical processes within lakes (Stephan et al. 1993, Blumberg and DeToro 1990). We plan to extend our studies to examine the decline of dissolved oxygen below the thermocline in summer and under the ice in winter. These simulations will be extended to simulate the distributions of fish and zooplankton in gradients of phytoplankton, light, temperature and dissolved oxygen using dynamic programming (Mangel and Clark 1988). Preliminary results are reported in DeStasio et al. (1996) and Hamilton and De Stasio (in press). Simulated distributions of physical and biological properties will be tested against observations from the NTL-LTER long-term datasets.

Expanding from our regional perspective (see Prior Research), we are coordinating an international workshop (to be held in 1996) on lake ice and climate variability (NSF Grant No. DEB 9416810). Our goal is to develop and analyze a hemispheric database on lake ice phenology, concurrent with our ongoing process-based modeling studies of the relationships between changes in lake ice and climate (Vavrus et al. 1996). We use lakes as indicators of climate variability and climatic change, and will advance our understanding of how changes in climatic forcing affect aquatic ecosystems globally through changes in ice cover and lake thermal structure.

b. What are the hydrological linkages between the atmosphere, terrestrial ecosystems and aquatic systems?

The supply of water to lakes results from complex interactions between the atmosphere, terrestrial ecosystems, and aquatic ecosystems. The regional hydrologic cycle is sensitive to variations in climate and changes in land cover. Increases in atmospheric CO2 may significantly change the water balance of the region by directly altering the composition, structure and water use efficiency of terrestrial vegetation (Field et al. 1995).

To improve our understanding of the regional hydrologic cycle, we will use a new, process-based, modeling system that is based on ongoing research at the University of Wisconsin-Madison. The cornerstone of the NTL hydrological modeling system will be the Integrated Biosphere Simulator (IBIS) (Foley et al. in prep.), which simulates terrestrial ecosystem processes, including evapotranspiration, photosynthesis, and net primary productivity. IBIS includes a multi-layer representation of soil moisture and thermodynamics, and an explicit representation of canopy photosynthesis and conductance (e.g., Farquhar et al. 1980, Collatz et al. 1991). To explicitly represent the dynamics of groundwater systems, we will directly couple IBIS to representations of groundwater hydrology. We already have extensive experience using groundwater models (e.g., MODFLOW) at our site (Cheng and Anderson 1992, 1993).

The modeling system will be integrated into our GIS-based datasets of topography, soil type, leaf area index (derived from Landsat-TM imagery - see Fassnacht 1995), substrate, and climate. We will operate the modeling system within a nested hierarchical grid: ~1 km resolution for the entire Great Lakes region; ~100 m resolution near our sites. The modeling system will operate on quasi-hourly timesteps to resolve important diurnal processes in the terrestrial energy, water, and carbon balance.

The NTL hydrological modeling system represents a unique tool with which to examine controls on the regional hydrologic cycle. With this system we can examine the sensitivity of watersheds and gauge the relative importance of: (1) seasonal and interannual climatic variability, (2) direct effects of increasing atmospheric CO2 on terrestrial vegetation and thus on the surface water balance, and (3) long-term changes in climate and land cover.

c. What are the biogeochemical linkages between terrestrial ecosystems and lakes?

Terrestrial biogeochemical processes strongly influence lake chemistry. In agricultural- and urban-dominated landscapes of southern Wisconsin, processes regulating overland movement of phosphorus are critical in regulating lake water quality (Soranno et al. 1996). In northern Wisconsin, groundwater exerts a major influence on lake chemistry (Webster et al. 1996). The chemical character of groundwater flowing into lakes is affected by the geochemical evolution of water as it moves through soils and tills (Kenoyer and Bowser 1992a,b).

We will assess the potential effects of land cover and terrestrial biogeochemical cycles on chemical inputs to lakes. In the Madison area, we will develop models that link land use and land cover to surface transport of phosphorus (see research area 5b and c, below).

In the Trout Lake Area, we will investigate the links between terrestrial vegetation, groundwater chemistry, and lakes. We will focus initially on how variations in climate and land cover might affect carbon budgets of lakes. Subsequently, we will turn our attention to nitrogen. Lakes are typically supersaturated in CO2, suggesting that influx of C from the landscape is an important part of a lake's C budget (Cole et al. 1995). For example, preliminary modeling of Sparkling Lake suggests that groundwater flow accounts for most of C input to the lake (Kratz et al. unpublished data). Groundwater flow and C chemistry are influenced by terrestrial processes occurring in soils and tills. We will continue our studies of soil respiration and N mineralization in soil, which vary strongly among forest types and affect the inputs of N and dissolved inorganic and organic C to groundwater and ultimately to lakes (Haynes and Gower 1995, Fassnacht and Gower unpublished). Estimates of detritus input, soil C fluxes, and N cycling processes (Running and Gower 1991) will be coupled with models of groundwater flow and chemical evolution (Cheng and Andersen 1992, 1993, Kenoyer and Bowser 1992a,b) to simulate effects of contrasting forest cover scenarios on inputs of inorganic and organic C and N to lakes.

Collectively, these efforts will initiate research toward an integrative, process-based view of the consequences of land cover change and forest ecosystem dynamics, for chemical fluxes to lakes. These modeling studies link atmospheric sciences, hydrology, biogeochemistry and limnology to analyze the regional dynamics of water and the solutes it carries. The mix of disciplines at our LTER site presents a unique opportunity to achieve this synthesis.

(5) Understand the ways human, hydrologic, and biogeochemical processes interact within the terrestrial landscape to affect lakes and the way lakes, in turn, influence these interactions.

Rationale and Background. It is no accident that native Americans and European settlers were attracted to the lakeshores and river valleys of the Upper Great Lakes region. As human use intensified, changes in freshwater ecosystems alarmed experienced scientists (Hasler 1947, Edmondson 1969). Veterans of ecosystem management find that environmental problems have multiple historical causes, and that integrated and interdisciplinary approaches are required for understanding (Gunderson et al. 1995). We have described integrative approaches to physical, chemical and biological processes at several important scales. We now turn to the feedbacks between these processes and society, which increasingly account for the nonlinear behavior and surprises that confound lake management.

Ecologists have long studied the complex hydrological and biogeochemical drivers that influence lakes (Wetzel 1983), and are increasingly aware of the predominant influences of humans (National Research Council 1992, Gleick 1993, Naiman et al. 1995). These forces suggest a feedback (which interacts with hydrological, biogeochemical and ecological factors) between human effects on lakes and behavioral responses of humans to lakes. For example, human-lake interactions are evident in the "leapfrog degradation" pattern found in recreational lake districts (Likens 1992). Lakeshore cottage development diminishes water clarity (Hutchinson et al. 1991, Naiman et al. 1995 p. 105), removes coarse woody debris essential for fish habitat (Christensen et al. 1996), increases angling effort (Stern and Stedman 1995) decreases catch rates (Carpenter et al. 1994), and causes trophic cascades (Kitchell and Carpenter 1993). In response to degrading lake conditions, cottage development expands to new lakes (Likens 1992).

***Proposed Research*.** We have selected five focal questions that require collaboration among specialists in demography, ecology, economics, history, and sociology.

a. What is the comprehensive history of settlement, city planning, urban growth, agricultural development, suburban expansion and recreation around the Madison lakes, and what is the impact of these cultural activities on limnological processes?

Since lake ecosystems are strongly influenced by history and are a product of both natural and cultural processes (Christensen 1989, McDonnell and Pickett 1993), detailed site histories of human activity around lakes should be developed to complement long-term data bases on hydrological and limnological processes.

We will develop an extensive environmental history of the Madison area lakes and watersheds. Our approach requires integration of the political, social, economic and cultural histories of the region's resources (White 1980, Langston 1995, Cullon 1995). For example, to survey land-use changes associated with urban growth we will incorporate histories of the regional economy, governmental regulations, infrastructure development, real estate markets and housing patterns. In addition to these political and economic dimensions of land use, cultural attributes of landscape preference such as parks, fisheries and even shopping malls need to be placed in their historical context, because shifting preferences influence development and protection of lake resources.

This analysis has at least two significant benefits. First, the history is a benchmark for scenarios and models of future land-use change, impacts on lakes, and lake management policy. Second, an environmental history provides a foundation for further research that connects environmental attitudes, behavior and economics to limnological processes.

b. How do lakes respond to reduction of nonpoint phosphorus pollution?

Although nonpoint P inputs account for most of the lake eutrophication in the United States, effective controls have proven elusive and mitigation programs are rarely evaluated (National Research Council 1992). We propose using a planned mitigation of nonpoint P inputs to Lake Mendota as an 18-year whole-lake experiment to measure effects of nonpoint P controls (Figure 17). The manipulation will begin in 1997 and continue for up to 12 years (Betz 1995). Landowners and municipalities, with cost sharing of up to 70% ($30 million) from the State of Wisconsin, will implement management practices designed to reduce P runoff by half. NTL-LTER will conduct the limnological studies, modeling and synthesis that make this manipulation an experiment. LTER staff have conducted the limnological analyses and modeling needed to plan the project, and worked closely with State and County staff in establishing the P loading target and project plan.

We will use a before-after-control-impact design (Stewart-Oaten et al. 1986), a standard for large-scale experimentation (Carpenter et al. 1995b). Reference ecosystems are Lake Wingra (urban catchment) and Fish Lake (agricultural catchment). The same variates will be measured in reference lakes and Lake Mendota, to check for regional trends that may affect our interpretation (Likens 1985, Stewart-Oaten et al. 1986). We will continue observations through the manipulation and for at least one hydraulic turnover period (6.5 years) after completion of the manipulation. Premanipulation P loads are known (Lathrop 1992, Soranno et al. 1996), and postmanipulation P loads will be measured periodically by the Wisconsin Department of Natural Resources in collaboration with the U.S. Geological Survey.

Our study will provide a comprehensive, interdisciplinary assessment of a large ecosystem management action. We will document the social context of management (see below), the changes in land cover and land use, changes in P loading, and limnological changes in nutrients, phytoplankton, zooplankton, macrophytes and fishes. Our findings will help guide future nonpoint P control programs throughout the world.

c. What is the spatial distribution of farmer behavior with respect to P fertilizer application, and what are the consequences for P inputs and watershed management policy?

Watershed policies and nonpoint pollution models make strong homogeneity assumptions. Lands are divided into a few coarse categories which are viewed as homogeneous for the purposes of analysis or management. However, farmer behaviors with respect to P fertilization are strikingly heterogeneous (Nowak et al. 1996). Typically, the distribution of P use by farmers in a given area is positively skewed, with both mean and median rates above the recommended level (Figure 18). Furthermore, P transport to surface waters depends on where, when and how it is applied on the landscape (Soranno et al. 1996). P transport models must therefore be based on spatial data, so that mitigation programs can focus on areas where excessive amounts of P are being applied to lands from which there is high transport to surface waters.

We will investigate behavioral heterogeneity in relation to P inputs in the Lake Mendota watershed. Survey instruments to measure salient P management behaviors will be used in conjunction with aerial photographs and GIS layers, and integrated with a spatially explicit P transport model (Poiani and Bedford 1995, Soranno et al. 1996). The result will be a validated simulation model that links the spatial distribution of farmer behavior to P transport. The instruments will also provide information about the rationales for P use decisions by farmers.

This analysis will quantify the consequences of spatial heterogeneity in P use for water quality. We hypothesize that a small percentage of farmers contributes disproportionately to P loading of Lake Mendota. Understanding the rationales behind this group's decisions will help design more efficient mitigation programs.

d. What are the relationships between human activity and limnological processes in a recreational lake district?

In recreational areas where human impacts are more modest, management could potentially sustain near-pristine conditions. Human activities with significant impacts in recreational lake districts include cottage development and fishing (Dillon and Rigler 1975, Larkin 1978, Hutchinson et al. 1991, Carpenter et al. 1994, Christensen et al. 1996). We will analyze the history of human activity in the Northern Highland Lake district over the past 50 years, and assess the relationship of human activity to limnological processes.

Analysis of human activity will be based on decennial censuses since 1940. This analysis requires two significant innovations. (1) We will develop and validate a procedure for allocating population and housing units to watersheds. For several test areas, we will overlay census polygons with watershed polygons. Using GIS, we will reaggregate population and housing data to watersheds using census street and road line segments, under the assumption that most housing units are near accessible roads. The method will be validated using visual image interpretation of air photos. (2) We will develop a procedure for inferring housing unit change since 1940 from data available in the 1990 census ("Year Housing Unit Built", Q. H17, long form). By successively removing more recently built housing from the GIS database, it is possible to synthesize housing unit density (and, with additional assumptions, population density) since 1940.

A comparative analysis of limnological characteristics will be conducted (Cole et al. 1991). Lakes will be selected from a gradient of housing unit density in the watershed. In these diverse lakes, we will measure fishing effort, fish population size structure, aspects of fish habitat (littoral macrophyte density and species composition, and coarse woody debris), zooplankton size structure, chlorophyll, color and nutrients.

Our analyses will reveal trends and spatial patterns of human activity (population, housing units, and their associated social and economic attributes) in the lake district, and their salient limnological correlates. The results will lead to more mechanistic analyses and modeling designed to project future trends in our study lakes of the Trout Lake region.

e. What are the implications of alternative land-use scenarios for the future condition of north temperate lakes?

As demographics and land-use patterns change, predicting the consequences for lakes becomes a key challenge. Our studies of interactions between humans and lake ecosystems and development of process models linking atmospheric, terrestrial and aquatic systems described above in research area 4 provide a strong foundation for comparing alternative scenarios.

We will develop spatially explicit models of land-use change linked to responses of water quality and fisheries for the Madison Lakes and for the Northern Highland Lake District. In Madison and its surrounding lands, rapid population growth and conversion of agricultural lands to urban uses are anticipated (DCRPC 1992). Alternative land-use plans are being considered in which locations of development vary and where development is spatially aggregated, dispersed, or funneled along corridors. These policy scenarios form the basis for our assessment of potential effects on lakes. In the Northern Highland Lake District, our model will focus on the expected increase of cottage homes built along the lakeshores and changes in land cover caused by forestry practices. We will employ (1) a probabilistic model that extrapolates past land-use changes into the future (e.g., Wear et al. in press), and (2) a process-based model (see research area 4, above) that describes movement of water and solutes from terrestrial to aquatic ecosystems. Both modeling approaches facilitate the exploration of planned alternatives in which reasonable policy options (e.g., cottage density limits, non-logged buffer areas around lakes) are imposed.

These modeling studies serve two important purposes. First, they provide an important mechanism for integrating our understanding of limnological processes and the activities of the human population in the region (Groffman and Likens 1994). Second, the models are potentially useful to managers as they strive to evaluate the ecological implications of alternative policy options.

Synthesis and Significance of Scientific Objectives

Fresh waters are central to the vitality of landscapes and society. During the next six years, we will build upon 15 years of LTER research to enhance understanding of lakes and their interactions with landscape, atmospheric, and human processes across multiples scales of space and time (Figure 19). We maintain our emphasis on the detection of long-term trends, the dynamics of within-lake processes, and the interaction between variability in space and time--recognized hallmarks of our ongoing LTER research. In addition, we continue to expand understanding of the dynamics of lakes within a regional context--the influences affecting lakes in different regions, how the relative importance of driving forces change with scale and the role of lakes as integrators of human activities (e.g., effects of diverse upland land-uses on aquatic processes) as well as their central role in focusing human activities in the landscape (e.g., through recreational uses and development).

The multiscale approach that characterizes our research is distinctive when compared to most research within limnology. Disciplines often focus on particular scales or levels of organization (Allen and Hoekstra 1992), but the need for research to bridge different scales as knowledge increases has become widely recognized (e.g., Levin 1992, Pickett et al. 1994). In spatial extent, we extend from individual lakes to the entire Upper Great Lakes region, with many of the focal processes spanning two or more of our four primary spatial scales (Figure 20). For example, we consider trophic interactions, nutrient cycling and biological invasions within individual lakes as well as multiple lakes. Similarly, analyses of temporal coherence span lake district and regional scales. We also study lake processes over a wide range of temporal scales (Figure 20). Biogeochemistry and groundwater dynamics, for example, are considered over time periods ranging from seasons to decades. Regional modeling of atmosphere-terrestrial-aquatic linkages spans the greatest temporal range, from within-year dynamics to centuries. We expect that our multiscaled approach, with its explicit recognition of scale-dependence for ecological processes, will yield a new integrative understanding of the long-term ecology of lakes.

We bring a plurality of approaches to our study of the long-term dynamics of temperate lakes. Long-term observations are crucial to the understanding of lake ecology and remain central to our research. For example, the invasion of Crystal Lake could not have been understood without our long-term data. However, our research is strengthened by a diversity of approaches that includes comparative studies among lakes and lake districts, experimental manipulations, and modeling. In our studies of temporal coherence, comparisons among individual lakes and across lake districts permit identification of similarities or differences in the state or dynamics of lakes, which in turn may lead to a general understanding of factors controlling different lake processes. Experimental manipulations help us develop causal explanations for observed patterns or phenomena (Pickett et al. 1994). For example, mesocosm experiments will reveal the degree to which C, N, and P may limit bacterial or algal growth. A large-scale experiment on reduction of nonpoint phosphorus pollution will yield in-depth understanding of the effects of a major manipulation relevant to resource and land management. Finally, modeling is an integral component of much of our work. Models will be used extensively at a variety of scales. Within individual lakes, models will contribute to understanding interactions between nutrient availability and food web structure, and we will apply inverse modeling (Parker 1977) to synthetic questions of comparative ecosystem ecology. Modeling is central to our attempt to integrate atmospheric, hydrologic and biotic processes at regional, lake district, and lake scales, to extrapolate our process-based understanding to lake-district and regional scales, and to project the likely consequences of land-use change on lakes. Collectively, our multiple and complementary approaches offer a powerful means to understand the ecology of freshwater inland lakes.

Several components of our research are of particular broad significance to ecology and ecosystem management. First, we anticipate our research yielding a new conceptualization of lake dynamics that is as powerful as the River Continuum Concept has been for flowing waters. We expect that our regional studies will provide further strong evidence of the importance of patterns and processes at broad spatial scales in explaining differences in the static and dynamic properties of lakes. Second, the knowledge gained and techniques developed for integrating ecological understanding of processes spanning broad spatial and temporal scales will be applicable to other ecosystems and regions. Third, we will forge new linkages between the natural and social sciences--a direction that is well recognized as a crucial challenge in understanding and managing ecological systems. Issues associated with ecosystem management, sustainability, conservation and economic development demand research across multiple scales and disciplines, and progress in science is often greatest where disciplines intersect (Pickett et al. 1994). Fourth, our enhanced understanding of aquatic systems and their interactions with atmospheric processes and regional biogeochemical cycles will offer a new perspective on the Upper Great Lakes Region.

Lakes are central and interactive components of the landscape. During the coming decades, lakes in the Upper Midwest are likely to experience increasing pressures as demands for sources of water and water use for agriculture, urban areas, and industry, as well as prime areas for recreation increase. Collectively, the understanding of landscape-lake-human interactions developed through our LTER research program will have direct relevance to development of policies affecting the future of the Upper Great Lakes Region and enhancement of the quality of life of its residents.

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Section 5. Project Management

Direction of NTL-LTER is provided by Magnuson with the participation of the Principal Investigators, research staff, and students. A subgroup of PIs act as an informal executive committee; usually, Magnuson, Bowser, Carpenter, Kratz, and Turner. All PIs meet monthly for one hour to plan and advise on program, personnel, and budget decisions; minutes are taken. We normal operate by consensus with Magnuson acting on hard choices. The entire group of researchers meet monthly for 3 hours to discuss concepts, present research results, and plan; minutes are taken.

Expansion of our research to the Great Lakes region through collaboration with two Canadian research groups is facilitated by an additional inter-site management team (Dillon - Dorset Research Centre, Hecky/Fee - Experimental

Lakes Area, and Carpenter, Kratz, and Magnuson). We routinely share data and are preparing joint papers. We have met twice and conducted a research workshop at Trout Lake with 12 scientists from NTL and 10 from the Experimental Lakes Area or Dorset. See Canadian letters of involvement on the back of the facing page.

Project Administration: The project is administered at the Center for Limnology (College of Letters and Sciences at the University of Wisconsin-Madison). The Center, directed by Magnuson, has field stations at both primary field sites, (Trout Lake Station in northern Wisconsin and Lake Mendota Laboratory in southern Wisconsin). Frost is responsible for the Trout Lake Station; Kitchell and Carpenter for the Mendota Laboratory. Both field sites have an LTER site manager (Kratz in the north; Lathrop in south) and LTER field technicians. Data management (Benson) is concentrated at the Lake Mendota Laboratory; remotely sensed data and GIS capabilities (Bolgrien) at the Environmental Remote Sensing Center directed by Lillesand. Water chemical analyses supervised by Bowser and Armstrong are in the Geochemistry Laboratory on campus. PIs are at both field stations or scattered across the Madison campus in three colleges and 9 departments. Most graduate students receive degrees in Oceanography and Limnology, Zoology, Water Chemistry, Environmental Monitoring, Botany, or Geology, but can come from any academic unit as our project evolves.

Project operations come from Magnuson, Egger and Wiedel and secretarial staff. Egger is the fiscal officer, Wiedel is a facilitator of meetings, research planning, and grant preparation. Secretarial and associated administrative activities come from Justice in Madison and Blair at Trout Lake.

The College of Letters and Sciences provides $422,683 direct costs annually for Center management and operations and general building services. Also a capital equipment exercise provides equipment to the research projects; remodeling moneys upgrade our facilities and housing. When direct costs paid by the college along with capital equipment and remodeling funds are accounted against the 43% overhead rate, the functional overhead rate on the LTER grant has been ca. 11% over the last 6 years.

PI Changes: Over the last six years one PI retired and 9 others joined; thus the number of PIs has doubled from our original 9. To accomplish our greater cross disciplinary objectives with the human sciences, we added 4 social scientists (Bill Cronon - environmental history, Tom Heberlein - environmental sociology, Peter Nowak - rural sociology and agricultural economics, and Paul Voss - human demography). We have also added four new colleagues interested in long-term regional ecology (Steve Carpenter - ecosystems, Stanley Dodson - zooplankton, Jon Foley - atmospheric sciences, and Monica Turner - landscape ecology). These people deeply enrich our program.

Site Leadership: Carpenter will take over the responsibility of Lead PI in a transition with Magnuson during 1997-98. Magnuson will remain as a PI until retirement in 2000. Bowser will retire at about the same time. Directorship of the Center for Limnology will pass from Magnuson to James F. Kitchell during a transition with Magnuson in 1999 and 2000. We are cognizant of these and other changes and are planning for them proactively.

Connectivity: Electronic connectivity is facilitated by Hanson at the Lake Mendota Laboratory. The Campus and the Trout Lake Station (approximately 4.5 hours drive distant) now are connected directly via Novell LAN, the university's ethernet, and a dedicated data line to the Internet. Figure 21 depicts the NTL-LTER computer facilities which links to Wide Area Nets. The Internet connection for the Trout Lake Station was completed in 1995. Researchers at both laboratories can access data and services from the NTL-LTER Oracle Server, the CFL file server, university libraries and departments, and Internet information servers, whether it is to send email, transfer files, share documents, or process administrative forms. Our researchers have the option of using Macintoshes, PCs, or Unix workstations without being restricted by file incompatibilities or operating system differences. Conferences and meetings are facilitated by telephone and computer conferences. This proposal, for example, was written from at least 5 remote sites with contributions and editing occurring on copies available to all on the Center for Limnology's Server.

Encouragement of Other Researchers: All PIs are at the University of Wisconsin-Madison; we have made 9 "non-LTER researchers" into "LTER researchers" in the last 2 years. We wrote 12 support letters for researchers at other Universities proposing to work at our site in the last three years. We encourage others by communications (posters

& talks) at national and international meetings; an excellent home page on the World Wide Web (http://limnosun.limnology.wisc.edu/); an open policy of sharing data in collaborative research; and by helping develop joint projects with scientist in USEPA (Little Rock Lake Acidification Project), USGS (Water Energy and Biogeochemical Budget - WEBB), Wisconsin Department of Natural Resources (Lake Mendota Watershed Project), regionalization to the Great Lakes Region (Ontario's Dorset and Canada's ELA) and CIC Universities (visiting graduate students), and other NSF programs (ROAs with Lawrence University), and LTER-associated NSF grants (Michigan Technological University, University of Wyoming, and University of Oregon).

Section 6. Data and Information Management

Philosophy and Goals Data management is an integral part of our research process. The NTL-LTER data and information system is designed to facilitate interdisciplinary research. From the design of data collection, to incorporation in the centralized database, to analyses, we focus on linkages among the components of the ecosystems we study.

Primary goals are to (1) maintain database integrity, (2) create a powerful and accessible environment for the retrieval of information, and (3) facilitate linkages among diverse data sets.

The data management group assesses data needs of the research team. This challenge is increasing as instrumentation and methodologies evolve. New technologies include Geographic Information Systems (GIS) for spatial data. We integrate these spatial data with core data to facilitate interdisciplinary research.

Response to Questions

1. How is the data manager involved in the design of research projects?

The data manager is a Ph.D. ecologist and is an active researcher on the project. She advises on the design of research projects and consults with students and other researchers on research data management.

2. What mechanisms do you employ to get researchers to contribute their data to the LTER database?

Core data sets are both collected and managed centrally as opposed to being collected and managed by individual PIs. Thus, at our site getting researchers to contribute data to the LTER database is not an issue.

3. How quickly are data sets made available to other researchers?

Meteorological and physical limnology are available within two months, fish data within four months, and other data including chemical limnology and other biological data within a year.

4. What criteria are used to limit or provide access of LTER data to other researchers?

We provide all core data on-line on the World Wide Web prior to the most recent five years with the exception of meteorological data which is placed on-line as soon as it has been incorporated into the LTER database (Table 1 shows the status). Our data access policy is available on our home page. Researchers who wish to access additional data or information must contact John Magnuson directly; we encourage collaborative explorations of our data (Table 2).

5. How often are data sets updated on the WWW?

Data sets are updated annually and whenever a database update affects data already on the WWW.

Personnel We have had the same data manager almost since the start of our project. This has provided us with stability and continuity. Two persons with backgrounds in computer science, databases and programming assist the data manager. Our remote sensing/GIS specialist has a Ph.D. in biology and is appointed jointly at the Center for Limnology and the Environmental Remote Sensing Center (ERSC). The system administrator at ERSC provides computer support to us. A full-time laboratory manager maintains the local area network and computers at the Center for Limnology. PIs have significant input to data management both in design and implementation

Data Sets and Availability A substantial part of core data collected by NTL (Table 3) reside in the Oracle database. Other data are maintained in text or spreadsheet format. NTL spatial data are stored on file systems at ERSC and are fully accessible to NTL researchers. Core data are available to all NTL-LTER researchers as soon as the data are entered and quality screened.

Data Access and Analysis We moved our database to a client/server environment to provide researchers with the powerful search and linkage capabilities of a relational database together with an end-user query tool for simple, direct access. A researcher may retrieve information from the database to answer requests such as "Produce the average epilimnetic chlorophyll concentration for a specific lake during the ice-free season for each year since 1982". The relational database supports the linking of the chlorophyll concentration table with the ice duration table, and the subsetting and aggregation that this request entails.

Our database server, Oracle7, resides on a Sun Sparc 10 workstation on our local area network. Currently, most researchers use an end-user query tool with a point-and-click type interface (available for both the PC and Macintosh). Oracle's Structured Query Language (SQL) capability provides cross-platform compatibililty.

Data management staff provide support to researchers in data analysis. Numerous programs have been written to manipulate raw data into forms requested by researchers (e.g., hypsometric averages of depth profile data, estimation of mixed layer depth, histograms of fish lengths). Views are created within the Oracle database to provide researchers with useful joins of the Oracle tables.

An alternative access system to data files in text format is available on our WWW home page (http://limnosun.limnology.wisc.edu) (Table 1). Links to on-line data are found within the on-line data catalog which supplies the supporting metadata.

Metadata Metadata are a crucial part of our information system. The data set catalog is on-line on the NTL-LTER home page. Each on-line data set contains header information (data set title, document update log, investigators, contact person, temporal and spatial resolution, descriptive abstract, study areas, variable description and units of measurement, variable codes, file format). Metadata for spatial data include copyrights, map scale, thematic and map accuracy, and data lineage information. Field and lab methods are documented for each core data set. Data management staff maintain a protocol notebook with schematic data flows, programs, and procedures.

Quality Assurance/Quality Control A number of different quality-control mechanisms have been established. For example, the sampling and analysis protocol for physical and chemical parameters includes random blind samples and replicate analyses at about the ratio of 1:10 (replicate:sample). Quality control in the chemical results are checked by ion balances, calculation of critical parameters from a redundant data set, and visual verification. Error checking occurs in the data entry software and proofreading. Finally, summary tables are reviewed by researchers.

Quality assurance (paper trail) for the data is handled by forms that accompany the samples from the field site through the lab. Data sets have a system of flags to indicate quality conditions such as: non-standard routine or equipment used.

Secure Storage The Oracle Server has functionality to maintain database integrity (passwords for access, privileges and roles to control read/write, recovery from system crashes, backup utilities). In addition to regular backups of the Sun system to 8 mm tape, we do a complete export of the Oracle database weekly. Copies of export files are stored on another server, on DAT tape, and on the Trout Lake Station file server. Data not currently incorporated into the Oracle database, are stored on a data management microcomputer with regular backups to tape. We maintain paper copies of all original data. ERSC makes backups of LTER spatial data to optical disk and tape. Image data are written to CD-ROM for long-term storage and retrieval.

Long-Term Maintenance Because the Oracle database is not appropriate for long-term archiving, we developed a script to write Oracle tables as external text files. We run this script when past year's data have been loaded into the Oracle database (or whenever we want an archive) and write the archive to CD-ROM.

Future Directions and Challenges We anticipate a long-term commitment to maintaining data sets on the WWW home page. The universal access of the WWW, makes our home page the likely main entry point for external data distribution. We will construct an interface between the WWW and part of our Oracle database to add query functionality to our data on the WWW.

The volume of spatial data, especially from satellite-based sensors, will increase tremendously over the period of the proposal. A first priority is to have appropriate data management in place. The same issues of needs assessment, data access, metadata, and database integrity will apply.

Intersite Data Management Contributions Our data manager is a member of Data Task, the steering committee for the LTER Data Managers, and helped organize the 1994 workshop entitled The Management of Spatial Data and Inter-Site Data Access in the Ecological Sciences (attended by representatives from agencies and other ecological research groups and the LTER data managers). She is a member of the LTER Network Information System working group.

Section 7. Outreach

NTL-LTER personnel engage in many important outreach and professional service activities.

Our program provides undergraduate students with extensive and rewarding first-hand research experiences. We involve 4 - 5 Research Experience for Undergraduate (REU) students every year in our summer LTER and related activities. We employ undergraduates as hourly workers to assist with summer field and laboratory work. We solicit applications for these positions from around the US and Canada. Our summer crews typically include an internationally diverse group. Many of our summer undergraduates continue on to graduate work in environmental science; we recruited several of these undergraduates to our own graduate programs. We encourage University of Wisconsin-Madison undergraduates to apply for university sponsored, summer environmental fellowships for independent research projects; at least one student was supported in each of the past five years. Their projects often result in publishable papers. A large number of graduate students and recent Ph.D.'s trace their roots to early experiences with the NTL-LTER program.

Graduate students are such an intrinsic component of NTL-LTER research that they figure prominently throughout our proposal. LTER funds supported 14 M.S. and 11 Ph.D. students over the past 6 years. These LTER-students have been highly successful in research productivity, in obtaining additional non-NTL-LTER support, and in obtaining post-graduate positions.

NTL-LTER investigators engage themselves in a wide range of public outreach activities. "College for Kids" program at the Lake Mendota Laboratory annually provides 20 4th and 5th grade students with hands-on, field-science experience. Our graduate students teach a summer enrichment course for disadvantaged and minority youngsters. Our researchers helped develop a limnology exhibit at the Madison Children's Museum. LTER investigators assisted in public presentations on applications of remote sensing by the Environmental Remote Sensing Center. Trout Lake workers participate annually in community activities such as the leading of popular nature walks, making public presentations on limnology and ecology, publishing a lake column in a local newspaper, and participating in a Northern-Highland-wide lake fair, where they have exposed local residents and visitors to a variety of aquatic organisms and processes.

NTL-LTER has taken advantage of ready access to the Internet system to develop accessibility to our activities, data, and information base. We have home pages for NTL-LTER (http://limnosun.limnology.wisc.edu/), the Center for Limnology (http://limnosun.limnology.wisc.edu/~webadmin/), and our Trout Lake Station (http://tk.troutlake.wisc.edu/).These pages are consulted frequently and the public now has ready access to most NTL-LTER data that are collected routinely (see Table 2).

NTL-LTER researchers participate in a wide range of professional service activities such as being participants or chairs for National Research Council committees, the FreshWater Imperative, State of Wisconsin Department of Natural Resources Committees, the Nature Conservancy, and the Leopold Memorial Reserve. We participated in the development of the National Center for Ecological Analysis and Synthesis. NTL-LTER personnel are active in national and international professional societies, particularly the Ecological Society of America and the American Society of Limnology and Oceanography. Editorial and planning services are frequent, e.g., our PIs chaired the local organizing committee for the 1993 ESA annual meeting held in Madison. We are frequent reviewers of grant proposals to the National Science Foundation and other funding agencies and routine participants on review panels. Many other such activities could be listed.