I. INTRODUCTION

We propose to continue our long-term ecological research on temperate lakes and their surrounding landscape in the Northern Highland Lake District of Wisconsin (Magnuson *et al*. 1984) as part of the national, Long-Term Ecological Research (LTER) network (Callahan 1984, Brenneman 1989, Magnuson and Bowser 1990, Franklin *et al*. 1990).

Our research expands upon the traditional boundaries of ecosystem studies to encompass multiple temporal and spatial scales. We consider a suite of adjacent lakes that share a common climate but differ dramatically in their physical, chemical, and biological characteristics. We employ a long-term perspective that permits us to place analyses of seasonal and annual patterns into the broader context of year-to-year variability and to evaluate the implications of such variability for community and ecosystem processes. We use a nested series of spatial scales ranging from within individual lakes to the entire Northern Highland Lake District (Appendix Fig. 1, p. 68). This permits us to consider how processes occurring in a lake are related to factors in adjacent systems and in the general landscape that surrounds it. Our broad temporal and spatial scales lend themselves to two expansions that we propose here; evaluations of the potential effects of global change and assessments of how processes discerned on smaller spatial scales are operating within the region in general.

Lakes provide ideal systems for long-term ecological research. Their boundaries are relatively distinct, and adjacent lakes, although sharing a common setting, may differ greatly in their fundamental properties. Thus, comparisons of lakes can be used to isolate at least partially important control factors for lake processes. Their distinct boundaries make lakes particularly useful for analyses of landscape-scale patterns. Likewise, many in-lake processes operate on shorter time scales than their analogs in terrestrial habitats (e.g., population growth and succession). This facilitates the observation of repeated sequences of processes within a few years as well as experimental manipulations. These advantages are coupled with a long tradition of limnological work which has laid a groundwork for our research. A substantial amount of this work was conducted on our LTER lakes by Birge, Juday and their colleagues in the first half of this century (Frey 1963, Beckel 1987).

In addition, because lake ecosystems superficially appear quite different from the principal ecosystems at the other, predominantly terrestrial LTER sites, the inclusion of the NTL site within the LTER network fosters the development of ecological theory at a more general level. Concepts that apply to both aquatic and terrestrial ecosystems must inherently have a broader applicability than those generated for a more restricted set of systems.

Within the synthetic goal of understanding the ecological complexity generated by multiple processes acting over many temporal and spatial scales, we aim to develop a series of broad-scale evaluations of factors controlling lake processes. These evaluations are interrelated but can also be considered independently. They can be classed generally into five major objectives:

- **A. To perceive long-term trends in physical, chemical, and biological properties of lake ecosystems**
- **B. To understand the dynamics of internal and external processes affecting lake ecosystems**
- **C. To analyze the temporal responses of lake ecosystems to disturbance and stress**
- **D. To evaluate the interaction between spatial heterogeneity and temporal variability of lake ecosystems**
- **E. To expand our understanding of lake-ecosystem properties to a broader, regional context.**

We elaborate on these objectives separately in the next five sections of the proposal. The first four objectives have played a key role in our research over the past five years. In discussing them, we highlight some of our major results and then outline the continuations that we propose. The last objective is new and reflects an expanded interest in seeking generality at both the site and the intersite level. Conceptual extensions within the first four objectives include 1) a focus on global climate change, 2) expanded evaluations of microbial processes and 3) more detailed assessments of land-water interactions.

II. SECTION 1 - RESEARCH PROGRESS AND PROPOSED RESEARCH

The following section describes our past progress and proposed research organized according to the five major research objectives listed above.

A. PERCEPTION OF LONG-TERM TRENDS

1. THE NORTH TEMPERATE LAKES DATA SYSTEM

Introduction. Our goal is and has been to develop a set of ecological measurements that will allow investigators quantitatively to observe and analyze patterns of long-term change in the physical, chemical, and biological features of lake ecosystems. We also wanted to make available the rich base of historic data collected earlier by E.A. Birge, C. Juday, and colleagues (Frey 1963). Finally, we wanted to establish an effective data management system to make the modern and historic data easily available to researchers.

Our choices of lakes and measurements were and continue to be guided by a desire to address important ecological and natural resource questions about lakes in respect to long-term (Likens 1983, LeCren 1984) and landscape level (Naveh and Lieberman 1984, Risser *et al.* 1984, Turner 1989) phenomena. These long-term measurements at various ecological levels and several temporal and spatial scales should be able to capture the essential structure and function of lake ecosystems and enable analyses of interactions among the principal ecosystem components.

Results. We have focused on a suite of lakes and surrounding terrestrial areas linked through a common groundwater and surface water flow system that share common climatic, edaphic, and biogeographic features (Fig. 1; Appendix Fig. 2, p. 69). The lake set includes oligotrophic, dystrophic, and mesotrophic lakes (Appendix Fig. 3, p. 70; Appendix Fig. 4, p. 71). Our seven primary lakes, located within 5.3 km of the Trout Lake Station in north central Wisconsin, were chosen to represent marked differences in size, morphometry and habitat diversity, in thermal and chemical features, in species richness and assemblies, and in biological productivity (Table 1, p. 3). The choice of primary lakes makes groundwater one major focus of our project, because of its importance in regulating differences in the chemical composition of lakes and in linking terrestrial and lake ecosystems (Likens *et al.* 1977, Winter 1978, Frape *et al.* 1984, Crowe and Schwartz 1981a, b).

We also have secondary lakes for which less complete data are collected. The choice of secondary lakes and types of measurements may change with time, but these lakes are studied with long-term research goals in mind. They serve for comparison with the primary lakes on specific research questions of individual investigators. For example Lake Mary, a meromictic lake, has the most temporally stable deep water system and is useful to compare with the other lakes which are influenced more by year-to-year changes in weather. Presently, our secondary lakes include: Clear, Escanaba, Fallison, Firefly (Weber), Little Rock, Mary, Mendota, Mystery, Nebish, and Pallette. Lake Mendota, our only study lake located outside the Northern Highland area, is included because the extensive and historical data available for Mendota are extremely valuable, one example being the use of ice cover duration to analyze climatic patterns (Robertson 1989, Magnuson 1990).

We spent considerable effort designing and implementing a balanced and integrated data collection program (Kratz *et al.* 1986). Our sampling (Appendix Table 2, p.83) allows comparisons of parameters among seasons, years, and lakes. We sample most major physical, chemical and biological parameters. On each lake we established a central station where related parameters are measured concurrently.

Sampling frequency is 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 cause severe stresses on biological components. Complete cation-anion balances are computed during these four periods. Nutrients, pH, inorganic and organic carbon are sampled monthly. Temperature, dissolved oxygen, chlorophyll *a*, primary productivity, and zooplankton abundance are measured every two weeks during the open water season and every 5 weeks under ice cover. 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. Typical sampling sites, from two of our LTER lakes, are shown in Fig. 2. In addition, groundwater levels in selected wells are measured monthly and groundwater chemistry from these wells is measured quarterly.

We maintain an automated land-based weather station 10 km from the Trout Lake Station. Parameters measured include air and soil temperature; precipitation; longwave, shortwave, and photosynthetically active radiation; wind speed and direction; and relative humidity. Our raft-based station on Sparkling Lake records air and water temperature, wind speed at three elevations, and relative humidity.

On occasion we have modified or developed measurement techniques. For example, we have developed state-of-the-art remote sensing for making acoustic estimates of distribution, abundance, and body sizes of pelagic fishes in conjunction with research sponsored by the Office of Naval Research (Clay 1983, Rudstam *et al.* 1987, Jacobson *et al.* 1989).

Proposed Research. We propose to continue the base sampling and data collection (Appendix Table 2, p. 83) started in the first 10 years (Magnuson *et al.* 1984, Kratz *et al.* 1986).

2. LONG-TERM DATA AND USE OF HISTORIC DATA

Introduction. We have access to three kinds of "long-term" data in our LTER project: data preserved in historical documents, data preserved in lake sediments, and data collected by the LTER program since 1981. Here, we provide examples of the types of analyses of long-term data that we have done using all three of these sources.

Comparing Recent Data with Historic Measurements. We used historic data spanning 1852 to present to analyze the link between ice cover of Lake Mendota and interannual variability in weather conditions including El Nino and climate change events. Unusual climatic conditions in areas adjacent to the equatorial Pacific Ocean have been shown to be directly related to El Nino events. Our goal was to determine whether El Nino events have influenced the climate of a more distant location, Wisconsin. We analyzed meteorological parameters and the long-term ice records with respect to the Southern Oscillation Index (SOI), a monthly correlate of El Nino intensity (Robertson 1989). Fourier Analysis, performed on the coinciding time series, demonstrated a relationship between ice duration on Lake Mendota and the SOI. After 1940, El Nino events are associated with consistent climatic anomalies (Fig. 3, p.6), warmer than normal December and March air temperatures with less than normal snowfall, resulting in late ice formation, early thaw and shorter than normal ice duration. Prior to 1940, El Nino events were associated with more variable climatic conditions. The ice conditions of Shell Lake, located in northern Wisconsin, were unrelated to El Nino events, possibly because Lake Superior's influence on local climate concealed signals from El Nino events.

We also related changes in lake temperature and ice cover to changes in mean air temperature associated with known and predicted changes in climate (Fig. 4). A step change in the duration of ice cover coincided with the end of the little ice age. We also forecast that if a 2XCO2 condition develops in the next 50 years due to Greenhouse Warming, Lake Mendota will be ice free 1 out of every 30 years by 2050 to 2060 (Robertson 1989).

Using the Sediment Record. We investigated the sedimentary record of pigments in short cores taken from Crystal, Sparkling, and Trout Lakes. Although diagenesis of pigments within the water column and sediments is significant, we were able to detect non-diagenetic trends (Hurley and Armstrong 1990b). Changes in the proportion of phaeophorbide suggest a period of reduced grazing starting about 1930. The concentration of diatoxanthin, a pigment associated with diatoms, increased sharply between 1900 and 1935 (Fig. 5) as did total phorbin and carotenoid pigment concentrations. This period corresponds to a time of clearcutting and may reflect response of Trout Lake to increased nutrient loading.

We discovered a relationship between a lake's dissolved silica concentration and the width of spicules growing in live sponges. Because sponge spicules are siliceous and well preserved in lake sediments we were able to use this relationship to reconstruct past silica concentrations in several lakes. We obtained complete sediment cores down to glacial material in three clearwater and six dystrophic lakes. In each lake there is evidence of a reduction in silica concentration over the holocene. Results from two dystrophic lakes are shown in Fig. 6. Groundwater is the major external source of silica to lakes in the region. The major sink is permanent burial in the sediments in the form of diatom frustules. Trends in silica suggest long-term changes in either groundwater inputs or internal cycling of silica, or both (p. 13).

Data Collected by the LTER Project. The LTER project has now collected nine years of data for many parameters. Here, we show three of the many examples of interesting patterns in this long term data set. In two of the examples, chloride concentration in Sparkling Lake (Fig. 7) and water level from three lakes (Fig. 8, p. 9) we have a reasonably detailed understanding of the underlying causes of the patterns. The chloride increase is associated with road salt entering the groundwater and entering Sparkling Lake (p. 15). The decrease in water level associated with lower than normal precipitation in the past few years is a function of the hydrologic setting of the lake and gives an example of how different lakes respond to the same climatic forcing. The third example, a decrease in silica concentration in Sparkling Lake (Fig. 9, p. 9), is an example of a trend that we do not understand sufficiently. Trends such as these, discovered serendipitously, are among the most intriguing and scientifically exciting.

Proposed Research. We will continue using historical archives, the sediment record, and the growing time series of LTER data to stimulate new questions and to ask and answer the questions developed in our major objectives. These data will be the basis for answering many of the research questions described in the next four major sections.

B. DYNAMICS OF EXTERNAL AND INTERNAL PROCESSES

Long-term patterns in lakes are generated by a complex interplay between external and internal processes. Evaluations of long-term patterns must be linked with an understanding of these processes. Because internal and external processes operate on a variety of time scales, interactions among them lead to complex patterns, often with time lags between cause and event. Understanding how lakes are affected by the interaction of process occurring on different time scales, particularly when there are time lags, is a major goal of our LTER program.

External processes influencing lakes include climatic and hydrologic factors combined with land-water interactions. Climate exhibits substantial year-to-year variation with potentially major effects on lake conditions (Madden 1977). Climate also exhibits distinct long-term cyclic behavior (Jones *et al.* 1982). Hydrologic differences among the NTL-LTER lakes are associated primarily with differences in groundwater inputs. These differences exert important influences on both water and chemical budgets. Variability in the groundwater system operates over a longer time frame than other components of the hydrologic budget such as precipitation and surface runoff. Land-water interactions involve linkages between terrestrial and aquatic systems in which numerous processes operate at fundamentally different time scales (contrast the growth and decomposition of trees versus phytoplankton).

Internal processes involve a diversity of physical, chemical, and biological factors. Again, the interplay of processes acting over different time scales leads to complex behavior. For example, a lake's primary production during mid-summer could be controlled directly by the extent of turnover during the previous spring and by the amount of grazing exhibited by herbivorous zooplankton during that period. Each of these processes in turn can be linked with longer-term factors such external nutrient loading and the year-class strengths of zooplanktivorous fishes. Consequently, primary production in one summer may be partly determined not only by present conditions, but also by year class formation of fish three years prior and the length of the turnover period in the previous spring.

A major goal of our LTER program is to develop a basic understanding of the roles of external and internal processes in influencing lake ecosystem conditions. Our primary efforts in this area include: 1) identification of major linkages between specific external or internal processes and limnological conditions, 2) evaluation of the interactions that occur among major external and internal processes, and 3) assessment of how long-term variability in specific processes influences long-term patterns in lake ecosystem parameters. Below we highlight separately some of our major research efforts on external and internal lake processes. This separation is not absolute but rather one of emphasis. Our goal has been to integrate both external and internal processes to generate a basic understanding of lake ecosystem processes.

1. External Processes

Our investigations of external lake processes have emphasized considerations of climate, groundwater hydrology, and land-water interactions.

a. Climate

Introduction. Climatic forcing controls the thermal environment of north temperate lakes by determining the timing of freeze and thaw, the length of the growing season, the depth of the mixed layer, the intensity of stratification, and the temperature of the various water layers. Thermal conditions form the setting for a lake's chemical and biological processes, many of which have rates dependent on water temperature. The LTER database is ideal for investigating the role of climatic variability in generating long-term trends in limnological processes (Robertson 1989) and in exploring relationships between climatic and non-climatic factors in lakes (Magnuson *et al*. 1990d). The threat of drastic climate change in the next century increases our incentive to learn about how lakes respond to climatic forcing. We will use the LTER database to develop and verify models of thermal, chemical, and biological conditions in the lakes relevant to global climate change.

Results. One emphasis of our climate research has focused on the effects of climatic factors on thermal conditions within lakes. Robertson (1989) used a long time series of ice cover records for Lake Mendota to reveal climatic variation on several time scales (Fig. 3, p. 6; Fig. 4, p. 7).

Robertson (1989) also demonstrated the utility of statistical and functional models in predicting thermal properties of lakes based on climatic variables. An empirical model employing meteorological conditions and water temperature successfully predicted the times of ice-on and ice-off for Lake Mendota. Climatic variables likewise showed the highest degree of temporal coherence in long-term comparisons across the LTER primary study lakes (Magnuson *et al*. 1990d).

Proposed Research. One of our long-range goals is to predict changes in limnological processes due to global climate change. This involves a three step process in which we 1) develop models of the influence of climate on thermal conditions within lakes, 2) predict the impacts of warming scenarios on lake conditions, and 3) examine the effects of predicted thermal conditions on internal lake processes.

What is the relation between climatic factors and thermal conditions in lakes? We will explore the relationship between climatic forcing and thermal response of lakes using functional and statistical models (Magnuson et al. 1990c). Modeling the annual thermal structure of the lakes requires predictions of the timing of ice formation and breakup, evaluation of heat exchange between the lake and atmosphere, and analysis of internal heat redistribution processes. For statistical models, we will employ the methods used to predict ice cover on the Lake Mendota (Robertson 1989) to develop similar models for other LTER lakes, using the historical meteorological database and ice cover records. We will also expand on existing functional models (e.g., Imberger and Patterson 1981) to predict the development of thermal conditions within lakes during the ice-free season. These models include explicit formulations of heat exchange at the air-water interface and between layers within the lake and predict thermocline depth and seasonal changes in epilimnetic and hypolimnetic temperatures. We intend to implement such models for several NTL LTER lakes.

How will thermal structure of lakes change following global climate warming? Using the models described above, we can create scenarios of the thermal structure of our lakes following global climate change using scenarios output from GCM's (e.g., Manabe and Stouffer 1980, Hansen *et al.* 1988). Transient climate warming scenarios are available representing the evolution of the global climate from $1XCO_2$ to $2XCO_2$ conditions. We will use these transient warming scenarios to predict the timing of thermal changes in our lakes.

How will lake processes respond to global climate warming? The chemical and biological responses of lakes to warming scenarios can be evaluated using models with varying levels of sophistication. Some models examine the influence of temperature on mass transport and kinetic interactions of biota and nutrients (Park *et al*. 1974, Blumberg and DiToro 1990). A relatively simple version of such a model might consider the dynamics of chlorophyll-a, carbon associated with zooplankton, phosphorus, nitrogen, silica, and dissolved oxygen. Such a model would be lake-specific and could be calibrated with LTER lake data. More detailed models could include the effects of individual species responses to changing thermal conditions. Several models incorporating these factors have been generated for lakes similar to those at our LTER site (Carpenter and Kitchell 1987).

The effects of global climate warming can be expected to be particularly strong on fish assemblages in north temperate lakes. The occurrence of fish assemblages in LTER lakes has been directly linked to the availability of suitable temperatures (McLain and Magnuson 1988). Bioenergetics models (Kitchell *et al.* 1977) can be used to produce scenarios of fish growth following climate warming (Hill and Magnuson 1990). Thermal niche models (Magnuson *et al.* 1990e) can provide estimates of changes in water volumes with temperatures suitable for different thermal guilds of fish (Magnuson *et al.* 1979). We will use changes in thermal niche space to forecast potential species extinctions or invasions in the lakes.

b. Hydrology

Introduction. Lakes within the NTL-LTER site vary markedly in the contributions of precipitation, groundwater, and surface water to the input portion of their hydrologic budgets. A strong gradient exists among our primary LTER study lakes that reflects increasing proportions of groundwater inputs (Okwueze 1983). This gradient has served as a major organizing theme in our program. We have examined this gradient's influence by 1) quantifying groundwater inputs, 2) determining the effect of groundwater on lake conditions, and 3) examining the role of groundwater in the transport of solutes, particularly nutrients and contaminants. We have emphasized studies of individual lakes. Success at this level permits us to expand our proposed efforts to a more regional scale.

Results. Quantitative hydrologic studies were initiated on Crystal Lake, which represents one extreme in the groundwater input gradient, with a marked predominance of precipitation inputs (Kenoyer 1986). Groundwater accounted for only 5% of input water to Crystal Lake, yet, because groundwater is more concentrated chemically than precipitation, groundwater accounted for substantial amounts of incoming solutes. For example, about 50% of the silica budget comes into the lake via groundwater, exerting a major influence on primary production in Crystal Lake (Table 2, p. 13) (Hurley *et al.* 1985). Detailed evaluations of groundwater flow paths confirmed that silicate hydrolysis in the glacial till surrounding the LTER lakes led to increasing concentrations of minerals with increasing time of groundwater contact with till (Fig. 10, Kenoyer *et al*. in press). Groundwater inputs to lakes like Crystal have the potential to vary substantially from year to year and provide a mechanism to control year-to-year differences in other lake parameters such as primary production or chlorophyll.

Sparkling Lake, lying at an intermediate elevation and with a presumed, higher proportional contribution of groundwater to its hydrologic inputs, was the next focus for quantitative evaluation. The more complex flow regime for Sparkling Lake, with substantial groundwater inputs and outputs led to the development of new techniques for quantifying hydrologic budgets. Stable isotope analyses of oxygen and hydrogen were coupled with more traditional, well measurements to evaluate the importance of groundwater in the lake's hydrologic budget (Krabbenhoft *et al*. in press a, b). We discovered that local groundwater had an isotopic signature distinct from mean annual precipitation values (Fig. 11). These differences exist because most inputs to the groundwater flow system occur during winter when the isotopic composition of precipitation differs from other seasons. During summer, precipitation is transpired and groundwater recharge is minimal. Models are being developed to examine the relationship between lake isotopic composition and the proportional contribution of groundwater to hydrologic inputs for lakes in general (McGrath *et al*. 1988).

Bog lakes at our LTER site are isolated to a large extent from surrounding groundwater flow systems. However, our studies have revealed that bog lakes exhibit a similar pattern, across landscapes, to that exhibited by the LTER lakes in general. The proportional input of groundwater to the bogs' hydrologic inputs increases with decreasing elevation in the landscape (Fig. 12, p. 15; Kratz and Medland in press). More detailed studies of Crystal Bog reveal a complex interplay between conditions in the lake and in the surrounding wetland due to the groundwater flow regime and resulting chemical transfers (Marin *et al.* in press).

The groundwater flow system can serve as either a barrier or a conduit to the transport of anthropogenic contaminants. The rate at which acid deposition falling within a region is transported to a lake varies substantially with hydrologic regime (Anderson and Bowser 1986). Because of buffering during groundwater flow, only lakes with a predominance of precipitation input would be expected to respond to acid deposition. In contrast, another contaminant, road salt, is transported fairly efficiently (Krabbenhoft and Bowser ms). This pathway has lead to a substantial systematic increase in the chloride concentration of Sparkling Lake since 1982. Even in the case of road salt, however, groundwater flow does not serve as a simple conduit. Increases in Na, the predominant cation paired with Cl in road salt, do not match those for Cl indicating that soil and aquifer ion-exchange processes are impeding its transport.

Proposed Research. Our goal is to integrate hydrologic studies with overall evaluations of lake conditions. This will involve two primary areas: continuing evaluations of the hydrologic budgets of individual lakes and expanding our hydrologic perspective to include a regional analysis of our entire study site.

What are the contributions of groundwater, precipitation, and surface flow to hydrologic and chemical budgets of Trout Lake? Our analyses of hydrologic inputs have moved from simpler to more complex systems. Trout Lake, the lowest elevation lake in our landscape, is the next logical choice for detailed study. The significant contribution of surface flow into Trout Lake will require an expansion of the methods that we have used for seepage lakes to include measurements of surface water flow. We will undertake these efforts in cooperation with the Wisconsin District of the U.S. Geological Survey.

Can stable isotope techniques be used to evaluate hydrologic processes for lakes and watersheds? Our work on Sparkling Lake has indicated the utility of stable isotope techniques for individual lakes, but the general applicability of these methods to larger scale systems remains to be explored. The stable isotope signature of oxygen and hydrogen of a water body at a particular time reflects an interplay between hydrologic processes that alter the proportions of stable isotopes and those that do not cause fractionation. Stable isotopes ratios are affected by evaporation but not by flow processes or transpiration. The degree of isotopic fractionation during evaporation varies as a function of temperature, relative humidity and the magnitude of evaporation itself. The isotopic signature of precipitation, in turn, varies with season and among storm events reflecting, in part, differences in evaporative processes.

The development of a general methodology for the use of stable isotopes in evaluating lake hydrology will require the cross-calibration of isotopic techniques with other more traditional measures of hydrologic parameters. We are expanding our measurements of such parameters for our LTER study lakes through the use of a combination of land-based and floating meteorological stations and expanded well networks. These measurements will be combined with previous hydrologic studies conducted near our LTER site (e.g., Little Rock Lake).

Stable isotope analyses will also provide insight into watershed processes. Summer precipitation appears to be largely captured and transpired by terrestrial vegetation, whereas winter precipitation is recharged into the groundwater system. Thus, with proper calibration, isotopic contrasts between local groundwater and rain should provide an estimate of long-term rates of terrestrial transpiration. This work will play an important role in our regionalization efforts (p. 42) and in our assessments of effects of global climate change (p. 10).

How are lake chemical conditions influenced by variability in groundwater inputs? Our work on lake/groundwater interactions has focussed on the chemistry of major ions and silica. We will expand these efforts to include assessments of additional elements, particularly N and P. By combining chemical analyses of groundwater, streamflow, and precipitation with the quantitative measures of these flows described above, we will be able to make direct assessments of their relative contributions to lake chemical budgets for the full range of lakes in our flow system.

We also will expand our work on the transport of contaminants by groundwater. The trends in Sparkling Lake's chemistry provide an ideal opportunity to examine these processes. The seasonally pulsed nature of road salt use may provide a particularly useful marker for examining trends in groundwater flow and in the transport of contaminants. This work will involve more detailed monitoring of wells near Sparkling Lake coupled with groundwater modeling.

c. Interaction between Terrestrial and Aquatic Ecosystems

Introduction. The NTL-LTER site is a mosaic of terrestrial and aquatic ecosystems (Appendix Fig. 1, p. 68) where terrestrial systems have the potential to exert major influences on lake conditions. Such terrestrial influences operate directly through the input of allochthonous materials and indirectly through an influence on hydrologic inputs. Characteristics of terrestrial ecosystems surrounding lakes, and their potential influence on lakes, vary as a function of soil substrate and natural and/or human-mediated disturbance regimes. Therefore, landscape position and disturbance regimes of terrestrial ecosystems must be considered in evaluating the factors influencing long-term patterns in aquatic ecosystems.

Results. Landform and soils vary greatly within the NTL-LTER study site reflecting past glacial history. Soils range from coarse sands with low water holding capacity and nutrient availability to fine loams with moderate to high water and nutrient availability (Appendix Fig. 5, p. 72). Several studies have demonstrated the relationship between soil characteristics and vegetation in the region (Curtis 1959, Kotar *et al.* 1988). Studies in the Pacific Northwest have demonstrated strong correlations between soil water availability and vegetational characteristics such as leaf area index (Grier and Running 1977, Gholz 1982) and net above-ground primary production (Gholz 1982). Vegetation is further influenced by disturbance and management regimes; these factors and their interaction have led to substantial differences in the vegetation surrounding the primary LTER study lakes (Appendix Fig. 5, p. 72) with important consequences for land-water interactions.

Allochthonous inputs add significant but varied quantities of carbon and nutrients to our study lakes (Appendix Fig. 6, p. 73). Perry and co-workers estimated that annual leaf litter inputs range from 400-1720 g/m of shoreline; annual phosphorus inputs associated with the fine litter ranged from 300-1470 mg/m of shoreline. The importance of leaf inputs varies among the LTER lakes owing to differences in landscape position, forest species composition along shorelines, and shoreline length relative to lake volume. Decay rates for allochthonous inputs also varied among lakes and with the species of source material.

Vegetational characteristics of the NTL-LTER site have undergone substantial changes over the past 125 years (Table 3). The pine forests that predominated in the region during presettlement times have been largely superseded by northern hardwoods (Morrison and Ribanszky 1989). Differences in vegetation also have the potential to influence the quantity and quality of groundwater flow within a region (as discussed above). These vegetation shifts have the potential to influence present day lake conditions with a variety of time lags. Shifts due to differences in the nature of allochthonous materials entering the lakes would occur within a few years for most materials. In contrast, there are substantial lags between the time water enters the groundwater and when it reaches a lake (Anderson and Bowser 1986).

Proposed Research. Expanded research here will focus on more detailed measures of the interaction between aquatic and terrestrial systems.

How does vegetation affect the hydrologic regimes of lakes? The absolute quantity of hydrologic inputs to lakes and the chemical characteristics of those inputs are influenced by the characteristics of terrestrial systems that surround them. For example, Swank and Douglas (1974) demonstrated that streamflow is greatly reduced by converting deciduous hardwood forests to pine due to the greater annual water losses via evapotranspiration in pine than deciduous hardwood forests. Borman and Likens (1979) observed a large increase in streamflow from a watershed that was harvested and noted that annual solute content in the stream was positively correlated to annual streamflow volume. We will develop a general model of the interplay between landform, vegetation, and hydrologic conditions for the NTL-LTER region.

Vegetational characteristics of the region will be determined through the use of remote sensing and GIS technologies (Appendix Fig. 5, p. 72). Preliminary studies suggest that the Landsat Thematic Mapper T can provide accurate hardwood vs. softwood and upland vs. lowland forest type separation (Hopkins *et al.* 1988, Morrison and

Ribanszky 1989). Researchers in the Environmental Remote Sensing Center will continue to develop systems for analyzing TM data using GIS technologies.

Leaf Area Index has proven to be a useful ecosystem parameter for comparing energy, mass, and water exchange across diverse ecosystems (Running *et al*. 1986, 1989; Running and Nemani 1988, Running and Coughlan 1988), and can be quantified by remote sensing, in some systems (Running *et al*. 1986, Peterson *et al*. 1987). Leaf Area Index will be combined with information on environmental factors in an ecosystem process model (FOREST-BGC, Running and Coughlan 1988) to estimate major water fluxes in terrestrial systems. This model was developed for coniferous forests and it will be modified for use with other forest types present at our site. Forest models will be combined with ongoing projects, funded separately by NSF

(to Gower *et al*.) to examine above- and below-ground carbon balances for terrestrial ecosystems.

What are the relative effects of allochthonous inputs of coarse woody and fine litter material on dynamics of lakes? Recent studies have demonstrated that coarse woody detritus can equal or exceed leaf litter input in some forest ecosystems (Vogt *et al.* 1986, Harmon *et al.* 1986). We propose to establish long-term plots along the shoreline of selected LTER lakes and bogs to estimate coarse woody detritus production. In addition, we plan to initiate a long-term woody decomposition study to estimate carbon and nutrient immobilization-mineralization patterns of woody material placed in lakes and bogs. This information will be combined with the studies on carbon dynamics described above and with the fine-litter detritus study by Perry.

How do long-term changes in terrestrial vegetation influence lakes? We will extend previous analyses of long-term changes in terrestrial vegetation for the regions adjacent to the seven LTER lakes and develop a more extensive analysis for northern Wisconsin. We will rely on historic vegetation surveys (Finley 1951) to recreate past vegetation patterns. Present conditions will be assessed using remote sensing and GIS technologies in conjunction with the modeling efforts discussed above. These data will be combined with our process oriented studies of terrestrial interaction with lakes (described above) to assess the importance of shifting landscape conditions on lakes.

2. Internal Lake Processes

Evaluations of internal processes emphasize controls over the phytoplankton, in terms of chlorophyll abundance and primary production, and the abundance of aquatic species in general.

a. Seasonal Chlorophyll Dynamics

Introduction. Chlorophyll density is a conspicuous lake feature controlled by an interplay of external and internal factors. At a given time, the standing biomass of chlorophyll within a lake results from an interaction of growth and loss processes. Differences in both growth rates, sometimes termed "bottom-up" control (Dillon and Rigler 1974, Schindler 1978, and McQueen *et al*. 1986), and loss rates, termed "top-down" control (Edmondson and Litt 1982, Shapiro and Wright 1984, Carpenter *et al*. 1985, 1987) have been shown to control chlorophyll biomass under some circumstances. It is unclear how the relative importance of these factors vary under natural conditions (Crowder *et al*. 1988), but models considering both bottom up and top down controls perform better that those focusing on either process alone (Carpenter *et al*. in press).

Results. Three LTER study lakes exhibit fundamental long-term differences in their seasonal chlorophyll dynamics. In Trout Lake, for every year between 1982 and 1989, spring and fall chlorophyll maxima are routinely punctuated by summer and winter minima (Fig. 13) in a pattern that is characteristic of many temperate-zone lakes (Hutchinson 1967, Marshall and Peters 1989). Two other lakes diverge from this pattern with reduced spring peaks in Allequash Lake in most years and with reduced fall peaks in Sparkling lakes in many years (Fig. 13). Can these differences, particularly the absence of a peak in some seasons, be attributed to a predominance of differences in growth or loss processes? Information on nutrients and zooplankton biomass indicate that they can not.

Reduced availabilities of nutrients in some seasons or years, owing to differences in mixing events or loading, would be a likely mechanism to lead to reduced chlorophyll levels through shifts in growth rates. Data on nitrate, used here as a general marker of the input of nutrients, indicates substantial year-to-year differences in peak concentrations in lakes and seasons (Fig. 14) but these differences are not correlated with peak chlorophyll concentrations. Shifts in the grazing pressure exerted by herbivorous zooplankton could also reduce chlorophyll levels through shifts in loss. Zooplankton biomass varies markedly across seasons and years in both Trout Lake and Sparkling Lake (Fig. 15, p. 23) but here too there is no correlation between chlorophyll and zooplankton.

Proposed Research *Can inter-lake and interannual differences in peak chlorophyll values be associated with shifts in growth processes or loss processes?*

Our approach involves combining our continued, long-term measurements of lake chlorophyll, nutrients, and zooplankton with a series of more detailed measurements of the nutrient and zooplankton dynamics taken during periods of increasing, maximum, and declining chlorophyll concentrations. We will focus on the epilimnion as a reasonable unit within which to develop a budget of the net interplay of growth and loss processes. The importance of nutrients will be assessed through experimental manipulations of nutrient availability along with direct assays for N and P stress. The influence of zooplankton will be evaluated directly using microcosms with various levels of grazing pressure (Lehman and Sandgren 1985). The role of mixing phenomena in controlling the availability of nutrients will be assessed through continuous monitoring of thermal profiles of our study systems. Funding to support our maximum expansion in this area has been requested in a separate proposal to the NSF Ecology Program (p. 118). If we fail to obtain that funding, we will conduct a reduced series of more detailed experiments and measurements than have been routinely included in our LTER sampling. **b. Controls on Primary Production**

Introduction. As in the case of chlorophyll biomass, the factors controlling a lake's primary production are a fundamental concern for aquatic ecosystem ecologists. We have focused on a subset of three of our primary study lakes to examine factors influencing production. The lakes were chosen to provide generally contrasting limnological conditions.

Results. Based upon several factors including secchi depths, major differences in groundwater inflow and associated solute loadings (Kratz *et al*. 1986), we had anticipated substantial differences in primary production among Crystal, Trout, and Sparkling Lakes. Several years of data on average daily rates of depth-integrated primary production, however, revealed remarkable similarities among the three lakes (117, 93, and 86 g C/m2/year for Trout, Sparkling, and Crystal (Adams *et al*. in press)). We have been examining the factors that account for this similarity, including possible differences in light penetration, similarities in nutrient loading particularly to the photic zone, and differences in internal nutrient cycling. Sampling for primary production is shown in Appendix Fig. 7, p. 74.

Light penetration varies substantially among Crystal, Sparkling and Trout Lakes with corresponding differences in the depth of the water column over which primary production occurs (Fig. 16, p. 24). Proportionally more production occurs at greater depths in Crystal Lake compensating for higher levels in shallower regions of Sparkling and Trout Lakes. These differences are attributable not only to differences in seston among the lakes but also to major differences in dissolved organic carbon (DOC). This DOC absorbs substantial quantities of light and competes with phytoplankton for light. A simulation in which the DOC in Crystal was increased to the levels that occur in Trout resulted in a 30 % decrease in calculated production (Kratz and Meinke, in prep.). Thus, relatively small differences in DOC may affect light penetration substantially and play a major role in regulating production in lakes where nutrient levels are low and photic zone may extend below the thermocline. Phytoplankton vary in their quantum use efficiency across lakes, with depth and with season. We expect this variation in how phytoplankton use light to be related to variability in primary production across lakes.

Similarities in production may also be related to nutrient inputs. Although groundwater inflow and solute loadings increase in the order Trout >Sparkling>>Crystal, the loading of limiting nutrients may be similar among the lakes. Low phosphate concentrations and high C/P ratios in seston (Hurley 1984) indicate P limitation during much of the year in all three lakes. P levels in groundwaters are low, and atmospheric deposition may be a relatively important external source of P, resulting in relatively similar areal loadings of P among the three lakes.

Internal cycling may also result in similar limiting nutrient loadings to the photic zones of the three lakes. Significant differences have been observed in the cycling of C, N, and P among the lakes. For carbon, sediment trap and bottom sediment accumulation rate measurements (Table 4, Hurley 1984 and NTL-LTER database) indicate high (> 50%) but similar decomposition rates in the sediments. Total water column respiration rates appear to be quite similar, but substantial differences in zooplankton biomass among lakes suggest that the proportion of carbon respired by zooplankton is much lower in Crystal than in Trout or Sparkling. This suggests that microbial respiration must be substantially higher in Crystal. These evaluations are only approximate and direct assessments of microbial respiration and production are planned to further ascertain the fate of produced carbon.

Internal cycling of P and N contrasts with that of C and exhibits substantial differences among Crystal, Sparkling and Trout Lakes. Low C/P ratios in bottom sediments as compared to seston reflect selective chemical immobilization of P in sediments (Table 5). C/P ratios higher than a Redfield proportion in Crystal Lake but substantially lower in Sparkling and Trout indicate that P is recycled much more efficiently from bottom sediments in Crystal Lake (Hurley 1984). Within the NTL-LTER region, the recycling of inorganic P from sediments has been linked with an interplay between Fe concentrations and the extent of anoxic conditions (Williams *et al.* 1971). These factors appear to be operating to generate the differences observed in P cycling within the LTER lakes. Evaluations of C/N ratios indicate that N cycling shows a similar pattern to that of P with a greater recycling of N in Crystal and Sparkling Lakes than in Trout.

Proposed Research. Our results to date indicate the influence of several factors in controlling the production of our study lakes. Evaluations of the interplay of these factors remain to be completed.

What is the role of nutrient loading to the photic zone in controlling primary production among lakes differing in groundwater inflow? With a database of several years on primary production and seston deposition from the water column combined with data on groundwater inflow, atmospheric deposition, and sedimentation rates, we are in position to evaluate the budgets of C, N, and P to the photic zone. We plan to develop ecosystem level models to evaluate these budgets for Crystal, Sparkling, and Trout Lakes. Several questions will be addressed: What are the relative nutrients fluxes from groundwater, atmospheric deposition, and internal recycling? Are year-to-year variations in fluxes appreciable? Is the flux of phosphorus limiting? Is immobilization of phosphorus in sediments a major factor regulating the phosphorus supply? What is the relative importance of regeneration within the water column (zooplankton, bacteria) and at the sediment-water interface (bacterial)?

To what extent does the proportion of primary production processed by zooplankton and the microbial food web vary among lakes? Estimates to date suggest that the relative proportion of carbon processed by microbes and zooplankton varies markedly across our study lakes. Our assessments have been limited, however, by a lack of direct measures of microbial processing. We propose to make direct determinations of microbial production and couple them with more detailed assessments of zooplankton grazing. This work will also be coupled with the nutrient budgets discussed above to evaluate the influence of microbes and zooplankton on primary production.

Bacterial production and respiration will be measured directly. Ideally, this work will be done in collaboration with Cole and Pace and/or with Dodson and Graham; both groups have grants pending at NSF to support this work. If their proposals are unsuccessful, more limited assessments will be made within our LTER program. Assessments of zooplankton effects will be expanded through the use of more detailed calculations based on species and size abundance data and size/species-specific respiration rates (Downing and Rigler 1984) and grazing rates (Sierszen and Frost In press), and through measurements of the proportion of chlorophyll *a* converted to phaeophorbide and collected in sedimentation traps (Hurley and Armstrong 1990a, 1990b). These data will be combined with carbon budgets of the water column, and fluxes of C into and accumulating in sediments to estimate bacterial respiration in sediments.

What is the role of P immobilization by Fe in limiting production in the NTL region? Our data suggest that P immobilization in sediments is strongly influenced by Fe, however, information on the role of Fe-P interactions relative to other factors limiting production is scarce. Measurements of the sedimentary component of C, N, P budgets combined with analyses of sedimentary inorganic P will be used to assess selective immobilization of P and its influence on regeneration of P relative to N (Armstrong *et al.* 1987). These evaluations will be expanded to include other lakes in the region with a wider range of Fe fluxes and sedimentary accumulation rates.

The influence of Fe on P release by sediments is strongly influenced by sediment anoxia. The potential for influences on the photic zone and primary production are high when P is released into the epilimnion or metalimnion. Thus, the sediment contact area in the metalimnetic zone plays an important role in seasonal internal cycling of P (Stauffer and Armstrong 1984). We will also investigate whether morphometry-related sedimentary P recycling plays an important role in the NTL region.

c. Shifts in Species Abundance

Introduction. Understanding the factors that control the presence or absence of species within an ecosystem is a fundamental goal for both ecological and evolutionary studies, particularly at a time when there is a major interest in the factors controlling the overall diversity of organisms. Moreover, studies of aquatic systems have revealed numerous cases where the abundance of particular species exerts a major influence on both community and ecosystem processes. Paine (1980) and Brooks and Dodson (1965), provided classic examples of fundamental shifts in community structure induced by single species and presaged numerous examples of the importance of such species driven processes (Stein *et al.* 1988). Hrbacek *et al.* (1961), Shapiro and Wright (1984), and Carpenter *et al.* (1987) have demonstrated that the effects of such species shifts can extend beyond community composition to exert a major influence over ecosystem processes.

Results. Within the LTER primary study lakes, our analyses of species abundance patterns have revealed that major species shifts are common. We have used these shifting abundance patterns, coupled with the comparative network provided by our lakes, to explore the factors controlling long-term variability in population levels. In addition, we have used these shifts to examine the impact of such changes on ecosystem processes and the importance of time lags that occur between events controlling a particular taxon and their subsequent effects on ecosystem processes.

Introductions of exotic species (e.g., rainbow smelt and rusty crayfish) into some of our LTER lakes provide, perhaps, the most dramatic cases of shifting species abundances (see Disturbance Section p. 30). In addition to these invasions, we have documented numerous instances where fish and zooplankton species have undergone shifts of greater than two orders of magnitude in abundance during a two to three year period. Crystal Lake provides a prime example. Here strong year classes of yellow perch in some years contrast with a nearly complete absence in other years. In other LTER lakes, other fishes, particularly zooplanktivorous cisco have undergone dramatic population shifts (Fig. 17). Similar patterns occur for zooplankton and benthic populations.

Situations where population levels are substantially different among years allow examination of factors controlling populations, particularly when the comparisons can be expanded to include two or more lakes. Shifts in cisco populations (Fig. 17) show the value of this approach. Autecological studies revealed that cisco require cold, oxygenated waters (Rudstam and Magnuson 1985). Such habitat conditions were met in Trout and Sparkling Lakes but were unavailable in Big Muskellunge Lake during 1982 (Fig. 18). Cisco were lost from Big Muskellunge Lake during this period but persisted in Trout and Sparkling Lakes. Thus cisco were excluded by physical and chemical conditions (McLain and Magnuson 1988). In a similar type of study, direct experimental analyses (Gonzalez 1988) showed that seasonal declines in rotifer populations were controlled by differing levels of food limitation. Broader comparative analyses have revealed the influence of varying silica levels on freshwater sponges (Frost and Elias in press) and the capacity of an animal-capturing plant to vary its investment in carnivory in direct response to differences in habitat conditions (Knight and Frost submitted).

Observations of Crystal Lake provide a strong example of the link between species shifts and ecosystem parameters. Adult yellow perch are zooplanktivores when they occur in a lake's pelagic zone. During years in which adult perch are abundant in the pelagic zone of Crystal Lake, the average concentration of the lakes dominant herbivore, a calanoid copepod, is markedly reduced (Fig. 19). Correlated with this reduction is a substantial decrease in the lake's water clarity attributable to a change in the standing biomass of primary producers. These shifts in water clarity appear to be influenced, at least in part, by events initiated two and three years prior to their impact (Magnuson 1990, Magnuson *et al*. 1990b). The abundance of adult yellow perch is linked directly to the success of year class recruitment, which is controlled by weather conditions during the first year of life. Thus, the shifts in water clarity observed in the lake are linked to external, climatic processes that operate with a two to three year time lag.

Proposed Research. Ultimately, a major goal of our research is to link separate studies of external and internal processes in a detailed evaluation of lake conditions. Shifts in species abundance with subsequent impacts on trophic interactions provide an organizing theme around which to build such a synthesis.

What is the relative role of external and internal factors in driving year-to-year differences in water clarity of Crystal Lake? As discussed above, we have observed substantial year-to-year differences in the secchi depth of Crystal Lake (Fig. 19). We have also identified two distinctly different mechanisms that could impart such year-to-year differences. Year classes of yellow perch can exert very different grazing pressures on the lake in different years. Likewise, year-to-year differences in groundwater inputs also have the potential to fuel substantially different levels of

primary production. We propose to integrate our measures of trophic and chemical effects on lake processes using similar models to those discussed in the Primary Production Section above. In particular we will contrast annual differences in top down control, as driven by fish, and bottom up control, as driven by differences in the quantity and quality of groundwater inputs.

C. RESPONSES TO DISTURBANCE AND STRESS

Perturbations affecting ecosystem processes operate on a broad range of time scales. On one extreme, some events, often termed disturbances (Pickett and White 1986), take place quickly but have effects that are longer lasting. In contrast, the effects of other perturbations, classified as stress, take place over an extended period. Stress and disturbance can be considered as two ends of a spectrum in which the time over which impact occurs varies. Understanding the role of both slow- and fast-acting perturbations is a fundamental goal in ecological studies (Connell 1978, Bender *et al*. 1984, Pickett and White 1986, Turner 1987). Our efforts at the NTL-LTER site have emphasized slower-acting perturbations, particularly acid deposition and species invasions. Our work on disturbance has considered the role of turnover events as disturbances in plankton communities and we are continuing these efforts in conjunction with our work on chlorophyll dynamics discussed above. Using a series of temporary ponds at the NTL-LTER site, we also have tested explicitly the hypothesis that the importance of biotic interactions in determining community structure increases with the extent of time between disturbance events.

1. Biological Invasions

Introduction. Lakes are island-like ecosystems (Fig. 20), isolated to varying extents from adjacent systems (Barbour and Brown 1974, Magnuson 1976). Natural immigrations of aquatic organisms are rare events, particularly where connections are limited among lakes. Such is the case at our site where five of our seven primary lakes are not connected by streams. Human-influenced species introductions, however, are generally much more common. To understand how species invasions affect lakes we need to answer two basic questions: 1) What factors control the probability of invasions into lakes? and 2) What are the effects of invasion on lake ecosystems?

The factors that control probability of the invasion of a habitat by a new species are poorly understood (Groves and Burdon 1986, Kornberg and Williamson 1986, Mooney and Drake 1986), but several studies suggest that perturbation leaves the ecosystem more vulnerable to invasion (Fox and Fox 1986, Orians 1986, Lawton and Brown 1986), through changes in resource availability or reductions in native species. We expect that climate change, a long-term perturbation, will affect the probability of species invasions in our lakes (Mandrak 1989).

The establishment of non-native species may have wide ranging effects (Simberloff 1981, Herbold and Moyle 1986, Moyle 1986, Vitousek 1986) . Such effects seem to be particularly likely in aquatic habitats where the substantial influence of trophic interactions is well demonstrated (Carpenter and Kitchell 1988).

Results. While there have been many species introductions within lakes at the NTL-LTER site over the past 80 years, primarily through fishery manipulations, three invading species stand out. Human activity has led to dispersal in our region of two crayfish species (*Orconectes propinquus* and *O. rusticus*) and one fish species, the rainbow smelt (*Osmerus mordax*). Of our primary study lakes, four have been invaded by *O. propinquus* (the earliest invader), two by *O. rusticus*, and two by smelt.

The effects of these invasions vary. We predicted that the invasion of smelt into Sparkling Lake in 1982 would result in the local extinction of cisco (*Coregonus artedii*), the native pelagic planktivore (Magnuson and Beckel 1985). Although extinction has not yet occurred, cisco are much less abundant and have suffered a near-total recruitment failure since smelt became abundant in the lake (Fig 21 top) (McLain and Magnuson 1988). In 1984 smelt invaded Crystal Lake, a small lake dominated by perch. So far there has been no significant change in perch abundance, and smelt have remained a small portion of the pelagic catch (Fig 21 bottom).

For the crayfishes, we predicted that the two invading species would become dominant sequentially, displacing the native species *Orconectes virilis* (Capelli 1982, Capelli and Magnuson 1983, Lodge *et al*. 1986). Typically the first invader, *O propinquus*, has not displaced the native species. In several of our lakes both continue to coexist. *O. rusticus*, which is more aggressive than the other species, overwhelmingly dominates in Sparkling Lake. In Trout Lake it has spread slowly, but where it is present it reaches abundances far higher than those of the other species (Fig. 22, p. 33). Experimental studies have shown that, at observed population levels, *O. rusticus* has the potential to exert a major influence over littoral zone communities (Lodge and Lorman 1987); however its impact under natural conditions remains to be demonstrated.

Proposed Research. We will continue to evaluate the effects of invading species on our study lakes. We also will focus on shifting patterns of invasion frequency and effect as they respond to environmental changes associated with climate.

How will climate associated changes in water levels and thermal regimes influence patterns of colonization and extinction? The rapid changes in climate anticipated in the next half-century (Manabe and Stouffer 1980) will likely cause a new set of stresses on the aquatic ecosystems at the NTL LTER site. These may include drops in water level both in our lakes and their associated wetlands, as well as changes in flow regimes. Increased temperatures are expected to alter thermal habitats, especially in the littoral zone and surface waters, where many organisms spend the larval life. Such additional pressures on the native communities may increase the probability of establishment of invading species and the extinction of native taxa, thus increasing the severity of the effects on the lakes.

We will approach this problem by using results from the regional hydrology (p. 42), thermal structure (p. 11), and water quality models (p. 44), along with our records of current species assemblages and habitat requirements to predict changes in associations in the LTER lakes. Ultimately we would like to generalize our findings to the entire lake district.

How will the spread of rusty crayfish affect the littoral zone communities in Trout Lake? We will continue to monitor the natural experiment of crayfish invasion and spread in Trout Lake. We have nearly annual crayfish distribution data dating back to 1970 and macrophyte and macroinvertebrate data starting in 1981. Collection of these detailed data will continue. Because the rusty crayfish has increased in abundance in the past few years, we expect to see shifts in littoral zone communities over the next several years.

What is the effect of macrophytes on their environment and other biota. Vegetation can effect the physical, chemical, and biological properties of the littoral zone (Lodge *et al*. 1988, Lodge and Lorman 1987). Consequentially the invading crayfish, *O. rusticus* by eliminating the macrophytes, can alter in significant ways the function of littoral communities. Obvious effects include loss of cover for fishes and habitats for macroinvertebrates. We will also examine the influence of the macrophytes on the oxygenation of the rooting zone (Jaynes and Carpenter 1986) and the subsequent influence of that on the fauna. A variety of differently vegetated habitats across the range of lakes will be compared, including the deep-water, poorly-illuminated submersed moss community below 10 m depth in Crystal Lake.

2. Acidic Deposition

Introduction. Acid deposition is an environmental stress of internationally recognized importance (National Academy of Sciences 1986, Altshuller and Lindhurst 1984). Lakes at the NTL-LTER site receive substantial acid loading (mean pH = 4.6 at the Trout Lake NADP Site) and many are classified as sensitive to the effects of acidification (Eilers *et al.* 1989, Watras and Frost 1989). Our research on acid deposition has focused on analysis of the role of groundwater buffering in mitigating acidification effects (p. 15) and on a whole-lake acidification experiment.

Results. The Little Rock Lake Experimental Acidification Project (LRL) was established to identify both the direct and indirect mechanisms by which increasing acidity affects population, community and ecosystem level conditions in lakes (Watras and Frost 1989). The program is funded by US-EPA and involves investigators from five institutions (Table 6). Little Rock Lake is a secondary LTER study lake that lies within the same groundwater system as our primary lakes. Sampling on Little Rock has been designed to parallel LTER efforts and there is close coordination between the two programs.

Following a baseline period, the two basins of Little Rock Lake were separated with a watertight curtain in fall 1984, and acid additions were begun to the north basin at ice-out in spring 1985. Our experimental design involves three, two-year acidification stages beginning at the lakes original pH of 6.1 and progressing through 5.6, 5.1 and 4.6. Baseline data collected prior to acidification indicated that the two lake basins were similar in physical, chemical, and biological conditions. Results after acidification indicated several distinct responses during the pH 5.6 stage (Table 7, p.

35) and an increased number at pH 5.1 (Table 8, p. 36). Data from the first year at pH 4.6 revealed in-lake conditions that were fundamentally different than those prior to acidification.

A key feature of the interplay between the LRL and LTER projects has been the development of general techniques for the evaluation of unreplicated, large-scale experiments. Experiments of this scale have considerable advantages (Schindler 1988) but they can only be interpreted against a background of natural variability (Frost *et al.* 1988). Data collected on LTER lakes in parallel with Little Rock Lake provide such critical information on natural variability. We are developing techniques to characterize this variability systematically (Kratz *et al*. 1987, Frost and Kratz in preparation). Much of this work has been conducted in collaboration with S. Carpenter who has been involved in whole-ecosystem manipulations on lakes nearby to our LTER site (e.g., Carpenter *et al*. 1989).

Proposed Research. Our efforts in this area will involve continued work on the influence of groundwater on lake acid-base conditions, the completion of the acidification stage of Little Rock Lake, and the initiation of a recovery experiment on Little Rock Lake (with non-LTER funding).

D. SPATIAL AND TEMPORAL VARIABILITY

Introduction. Traditionally, lake studies have emphasized heterogeneity 1) within lakes and within years, 2) among lakes for a limited number of years, or 3) among years for single lakes. Our study differs from these in that it examines seven lakes over the long term. A major strength of our approach is that we can consider multiple scales of spatial and temporal variability and interactions not only between spatial and temporal variability, but also between perceptions of variability and scale of observation. We can also take advantage of the LTER network to compare patterns of variability observed in lakes to patterns observed in other ecosystem types.

Variability is an inherent characteristic of all ecosystems, yet there is little understanding of how systems differ from each other in variability patterns, or what factors might lead to these differences. Technologies such as remote sensing and geographical information systems allow us to sample and analyze different systems at the same spatial scale. Use of these tools can be particularly powerful in the analysis of landscape structure of diverse systems.

Temporal variability arises through the interplay between internal dynamics and fluctuations in external driving forces. Non-equilibrium concepts are often more useful in studying ecosystems than equilibrium constructs (DeAngelis and Waterhouse 1987, O'Neill *et al*. 1986). Understanding the constraints on ecosystem behavior and characterizing an ecosystem's behavior prior to stress are important foci for analyzing temporal variability.

Spatial heterogeneity may interact with temporal variability in determining community and ecosystem features. A spatially heterogeneous environment can be an important factor in determining and maintaining community organization (Sale 1977, Whittaker and Levin 1977, Levin 1978, McNaughton 1983). Spatial heterogeneity may decrease the connectedness of a system and act as a buffer against disturbance. Alternatively decreased connectedness may prevent the reinvasion of a species lost after a disturbance.

Results. Our efforts to date have been focused on three general areas.

First, we focused on variability patterns of limnological parameters. We developed techniques to determine the degree of year versus lake specificity of these parameters (Kratz *et al*. 1987, Frost and Kratz manuscript). In general, we found that most lake parameters exhibited more lake specificity than year specificity (Magnuson *et al*. 1990b). However, those parameters exhibiting year specificity were linked to weather related processes (Fig. 23). These parameters included lake water level, ice duration, and concentration of chemical parameters whose major source is precipitation (pH, SO4). Interestingly, rotifers, zooplanktors with short generation times and high reproductive potential, also exhibited year specificity, suggesting they can adapt quickly to favorable climatic conditions (Kratz *et al*. 1987). We also have used these analyses of variability patterns to aid the interpretation of results from whole lake experiments (Carpenter *et al.* 1989, Frost and Montz 1988).

Second, we focused on the variability patterns of systems and asked whether differences in the variability patterns exhibited by different systems (different lakes within our site as well as different LTER sites as a whole) could be related to physical, chemical, or biological properties of the sites. We approached this question at two levels. First, we compared the variability patterns observed in our seven study lakes. We found that a lake's position in the landscape and the relative importance of groundwater inflow were good predictors of the variability of edaphic parameters in the lakes (Kratz *et al.* submitted manuscript) (Fig. 24, p. 38). Furthermore, we found that variability patterns associated with elevation in the landscape were also evident at three other LTER sites, Jornada, North Inlet, and Hubbard Brook. In all cases water movement was an important determinant of the variability patterns observed (Kratz *et al.* submitted manuscript). At the second level we compared variability patterns of 12 LTER sites (p. 54, documentation in Appendix Table 3, p. 86). Here the comparison was one of desert vs lake vs forest vs stream etc. We found that the 12 LTER sites differed in their variabilities (Fig. 25, p. 38), and the magnitude of spatial and temporal variability may be related negatively to the productivity of the site (Kratz *et al.* manuscript). We also found that when parameters from all 12 LTER sites were taken as a whole, spatial variability was larger than temporal variability, and biological parameters tended to be more variable than climatic or edaphic ones (Fig. 26, p.39) (Magnuson *et al.* 1990b).

Finally, we focused on how the physical heterogeneity of a system affects the biotic community structure. We examined the temporal and spatial variability of the littoral zone fish communities at two different spatial scales: among lake and within lake. Interyear similarities in fish community composition for individual lakes were twice the interlake similarities. Based on observed similarities or on simulations, we concluded the similarities were influenced by species richness, the probability of strong year classes, and dominance and age structure of the assemblages (Benson et al. manuscript). The degree of within lake spatial heterogeneity in species composition differed among lakes and was positively correlated with the shoreline development index, substrate diversity, depth diversity and species richness (Benson and Magnuson, manuscript).

Proposed Research. Our proposed research is focused on two major areas: 1) understanding what features of lakes control temporal heterogeneity in biological parameters and processes, 2) how landscape structure and scale of observation interact to affect our perception of spatial heterogeneity of broad areas.

What characteristics of lakes control temporal variability of limnological parameters? In particular, do lakes with simple fish communities (few taxa) show higher variability in populations and production than lakes with complex fish communities (many taxa), and to what degree does landscape position influence the temporal variance of biological parameters? We hypothesize that landscape position, exposure to climatic factors (i.e. morphometry) and complexity of the fish community structure are three features of lakes that exert important, and potentially interacting, influences over temporal variability within our LTER lakes. We have shown that lakes high in the groundwater flow system, additionally characterized by simple fish

communities (e.g. Crystal Lake), exhibit more annual variability in chemical parameters than lakes lower in the flow system with more complex community structure (e.g. Trout Lake). We will extend our analyses to include exposure to climatic factors and analyze variability patterns in a suite of biological parameters representing all trophic levels in the lakes.

Is the landscape structure of land islands in water the same as that of water islands in a matrix of land? The structure of land patches imbedded in a matrix of water and water patches in a matrix of land can be compared quantitatively using measures derived from landscape ecology (Naveh and Libermann 1984, Risser *et al*. 1984, Forman and Godron 1986, Franklin and Forman 1987, O'Neill *et al.* 1988). As the proportion of land to water grades from 100% water through island archipelagos and lake districts to 100% land, the properties of the two systems might become transposed. A null hypothesis would be that the transposition is symmetrical, i.e. water patches at 25% water would have the same character of land patches at 25% land or at 50% land and water the structure of the two systems would be the same. This transposition of character can be examined at several scales using routines available in geographic information systems. Measures to examine this hypothesis include size and shape of patches, the proportion of interior versus edge habitat, and fractal dimensions as well as relational measures such as connectedness, texture, interpatch distances, fragmentation, general impedance to movement, and anisotropy.

What are the effects of grain and extent on perception of patchiness of chlorophyll in lakes and forests? One important consideration of comparing divergent systems is the ability to observe them at the same spatial scale (Magnuson 1988) or better yet in a nested set of spatial scales. Technologies are available to contrast the patchiness of chlorophyll in terrestrial and aquatic systems at the same spatial scales, for example remote sensing with AVHRR, Landsat or SPOT. There should be basic differences in the patterns of plant distribution on the surfaces of terrestrial and aquatic environments; a major component of terrestrial vegetation patchiness is closely related to rather permanent landforms and edaphic factors while surface chlorophyll distributions of lakes and oceans are closely tied to dynamic currents, eddies, upwellings, convergences and fronts. Without including the structural features of patchiness in aquatic systems, a landscape view of the surface of the earth is incomplete. We expect that a formal quantitative analyses of these structures at the same set of nested spatial scales will lead to conceptual advances in this area.

Our approach will be to compare the patch statistics such as those we have developed (Nero and Magnuson 1989) for acoustic remote sensing as a function of changes in grain and extent. The influence of extent will be especially interesting because we will contrast bounded (island and small lake) with images of the same extent from unbounded systems (continental forests and large lakes or possibly oceans). For lakes we will use the Northern Highland lake district including the LTER lakes and Lake Michigan; for land we will use the Great Lakes forest in the Northern Highlands lake district and islands in Lake of the Woods and Lake Superior.

E. REGIONALIZE TO BROADER SPATIAL SCALES

Introduction. Of particular interest during the proposed grant period is the issue of how to make useful predictions across different scales (references in Landscape Ecology. 1989. 3(1-2)). We wish to scale-up from the seven LTER lake area to the Northern Highland Lake District to assess: 1) how well we can transfer our understanding of processes within the LTER lakes to a larger region, 2) regional impacts of global change, 3) regional diversity, 4) effects of regional changes in conservation, forestry, land development, and recreation policies.

Although problems of scale have always been part of ecology, scale has received particular attention in recent years through the application of hierarchy theory (Allen and Starr 1982, Levandowsky and White 1977, O'Neill *et al.* 1986, Allen and Hoekstra 1990). Hierarchy theory provides a particularly useful conceptual framework for LTER because it contains a coherent view of the nature of ecological complexity, it explicitly analyzes the role of the extent and grain of the observation set in long-term observation, and it may generate unifying principles for the entire LTER program because all LTER sites study systems at multiple scales.

We do not believe that simply extrapolating across scales will be an effective means of predicting across scales. For example, analyses of satellite and acoustic remote sensing scenes makes clear that interesting differences result when the natural world is viewed at different scales. We examined the distribution and morphometry of our lakes from the grain of a Landsat TM image (30 m) to that of an AVHRR image (1 km) (Fig. 27). In this case, information was lost as we shifted to the coarser grain; this is important to the interpretation and evaluation of a lake district.

Many of the features are only observable at the finer scales (97% of the lakes disappear between the 30m and the 1km scales) and significant bias develops in the parameterization of the objects of interest. For example, the average lake area increased from 9 to 240 ha and fractal dimension from 1.22 to 1.26. The results from the acoustic remote sensing are perhaps more interesting (Fig. 28, p. 42), here different features of the patchiness of nekton and macrozooplankton are apparent at the different grains of analysis (Magnuson *et al*. 1990b, Nero and Magnuson 1989). At the finer scale, patches of organisms are visible which probably represent behaviorally mediated aggregations of species or assemblages; at intermediate grain, patches reflect the major physical gradients in the scene (i.e. the Gulf Stream front) and at the coarsest grain, patches reflect the concentration of organisms in the different water masses. The acoustic remote sensing equipment used to collect these data is the same as we use in the annual census of pelagic fishes in each of the LTER lakes.

In many ways we face the same dilemma as molecular biologists using their methodology to predict the behavior of communities of organisms or as population ecologists using their methodologies to predict the functioning of organ systems. For the present, it seems clear that (1) structural analyses must be conducted across scales at least until we obtain a better understanding of how our view of the natural world is affected by scale of observation and (2) we must develop sets of appropriately scaled models to cover a range of spatial grains and extents. To address the first we will continue to use remotely sensed data to test how perception of landscape structure changes as a function of grain and extent of observation. In addition, we will use our nine years of relatively fine grain temporal data to test how changing temporal grain of observation influences our interpretation of limnological behavior. We will address the second in two new initiatives: development of a spatially explicit regional hydrologic model and development of a model predicting chlorophyll concentrations and water color of lakes from landscape features.

1. Regional Hydrologic Model

Introduction. Hydrologic processes provide a major linkage between aquatic and terrestrial systems. Our study lakes are surrounded by a diverse landscape, comprised of a mosaic of different soil types and conifer and deciduous forests of varying successional status. Because different vegetation and soil types have different rates of evapotranspiration, one important influence the vegetation and soils have on lakes is their effect on lake and groundwater levels. To develop better our understanding of terrestrial/aquatic interactions and to provide a template on which we can assess landscape level impacts of global change, we propose to develop a spatially explicit hydrologic model for the Northern Highland Lake District.

Results. Our detailed understanding of groundwater hydrology of Crystal and Sparkling Lakes provides an excellent base from which to develop a regional hydrologic model (p. 13). We have completed work of a more regional nature as well. Okwueze (1983) has mapped the groundwater level over a 100 km2 area, and Kratz and Medland (in press) have shown how groundwater inflow into ten kettle-hole peatlands is a function of the peatland's landscape position.

Proposed Research. We will focus on two questions. The first considers the process of expanding the spatial scale of our analyses. The second considers implications of global change on regional hydrology.

Can a regional hydrologic model be developed as a synthetic tool for understanding terrestrial/aquatic interactions? We propose to develop a spatially explicit, groundwater model (using a two-dimensional application of MODFLOW, the USGS computer code developed by McDonald and Harbaugh (1988)) linked to a terrestrial ecosystem model that computes evapotranspiration. We will develop a nested series of groundwater submodels that will allow us to view the system on a variety of spatial scales within the Northern Highlands Lake District. We will test whether our understanding groundwater flow and lake evaporation derived from studies on single lakes is sufficient to generalize to broader regions.

The model simulating evapotranspiration (FOREST-BGC, cf Running and Coughlan 1988) will be developed by Gower as described on page 19 for red pine stands. Subsequent development of the model for other cover types will follow as rapidly as funding allows.

The linked hydrologic model will use input data from a GIS database that we propose to develop from existing information on regional hydrology and soils, supplemented by additional measurements of lake levels and streamflow. The models will be linked through the evapotranspiration term. Specifically, the source term to the groundwater model, groundwater recharge, will be calculated as precipitation minus evapotranspiration and surface water runoff (streamflow). The final output from the model will be the spatial and temporal distribution of groundwater levels.

Initial model validation will be based on the model's ability to predict current lake levels of 1) the seven LTER lakes and 2) lakes in adjacent groundwatersheds. Validation will be supplemented by estimates of groundwater fluxes and lake evaporation calculated from stable isotope measurements taken from a selected sample of lakes in the region.

We plan to use the spatially explicit hydrologic model to assess scenarios of global change and to assess changes in chemical loading to lakes via groundwater. Here, we use the phrase "global change" to encompass both climate change as well as shifts in land use in our region.

How will global change affect water table and lake levels, lake-connectedness, and the relative percentages of land, lakes, and wetlands? We will use the regional hydrologic models to simulate response of water level to different climatic scenarios. We will couple model output with our geographic information system to quantify how changes in water level will affect surface water connections between lakes and the relative areas of land, lake, and wetlands. These analyses will provide the basis for further exploration of effects of global change on the Northern Highland Lake District landscape.

2. Regional Model of Water Quality

Introduction. A useful approach to regionalizing our understanding of processes affecting lakes is to develop models to predict lake characteristics based on a lake's morphometry and physical position in the surrounding landscape. Such a model could be used in conjunction with data derived from satellite remote sensing to assess

lake characteristics over an extended region. We propose to develop a model to predict surface chlorophyll *a* concentration and water color. These two parameters are particularly well suited for this type of analysis because: 1) they are both fundamentally important characteristics of water bodies, 2) they are both amenable to remote sensing via satellite (Appendix Fig. 8, p. 75). In addition, this work will complement our studies of the factors determining seasonal patterns of chlorophyll distribution (page 21). Although we expect that processes internal to lakes are important determinants of chlorophyll and water color, we expect that strong external influences also exist. For example, surface chlorophyll concentrations depend to a certain extent on nutrient budgets of lakes which, at our site, depend on the position of the lake in the landscape, the proportion of the water budget coming from groundwater versus precipitation and other factors. Water color is strongly influenced by the quantity of *Sphagnum* wetlands surrounding the lake and the lake's water turnover time (Gorham *et al*. 1986).

Results. Previous work has stressed the importance of chlorophyll and water color as limnological parameters in our lakes. Chlorophyll, as a measure of phytoplankton biomass describes a basic element in a lake's trophic dynamics (page 21). Water color, through its influence on thermal properties and light penetration, has important effects on lake primary production (page 23). We have demonstrated our ability to measure these parameters by satellite remote sensing by calibrating the Landsat data with direct *in situ* measurements made at the time of the overflights (Lillesand *et al*. 1983, Lathrop and Lillesand 1986). Regressions of landsat thematic mapper T Band 3/Band 1 ratio were found to predict the natural log of water color in a study of 23 lakes within the LTER study area (Lillesand *et al.* 1989, Morrison and Ribanszky 1989).

Proposed Research. Can surface chlorophyll and water color of lakes be modeled from lake morphometry and characteristics of the surrounding landscape? We propose to develop a model predicting the surface chlorophyll concentrations and water color of lakes across the Northern Highlands Lake District as a function of landscape characteristics and then verify the model with measurements from our LTER lakes and satellite remote sensing of lakes through the region. We will devise a model for which the input parameters can be sensed from satellite images and processed automatically from the digitized data bases. Initially, direct measurements of the 7 primary LTER lakes will be compared with the model output and the limnological basis of the model will be reevaluated. Then to test the revised model, lake color and chlorophyll concentrations will be compared for lakes over a larger portion of the lake district. Again the model will be modified and the results compared with another set of lakes in the district. The purposes are to develop a model suitable for regional extrapolation and to analyze whether we understand and can remotely sense the factors which determine water quality over a broad region.

III SECTION 2 - ELEVEN TOPICS

1. FIVE CORE AREAS

Although the research approach that we have used to organize our proposal is not directly tied to the five core LTER areas, most of our effort can be categorized within the core framework. Here, we indicate explicitly the research we are conducting in each of the core areas and refer the reader to specific pages in the proposal for more detailed information.

Pattern and control of primary production. Understanding the factors influencing primary production in lakes has been and continues to be a major goal of our program. A major section of our proposal is devoted to this topic (p. 23).

Spatial and temporal distribution of populations selected to represent trophic structure. This is another area of major emphasis. One example of our work in this area is the study of the trophic dynamics in Crystal Lake (p. 29). Other examples include our work on how heterogeneity of physical environment affects the distribution and temporal variability of populations (p. 37) and our work on understanding the effects of species invasions into our study lakes (p. 30).

Pattern and control of organic matter accumulation in surface layers and in sediments. We address this topic in four ways. First, we continue to use the sediment record in our lakes to infer past processes. Currently, we are using fossil pigments and sponge spicules to infer past trophic conditions and past silica concentrations (p. 7). Second, we are investigating how allochthonous input of leaves to littoral zone surface sediments influence nutrient budgets in our lakes (p. 18). Third, we are examining the role of pelagic sediments as a source of nutrients to the water column via regeneration (p. 24). Fourth, we are participating in the intersite leaf decomposition experiment (p. 56) and plan an experiment with coarse woody debris (p. 20).

Patterns in inorganic inputs and movement of nutrients through soils, groundwater, and surface water. Hydrologic studies, emphasizing groundwater flow, have played a critical role in our overall research theme (p. 13). In particular, the transport of nutrients within various hydrologic flow has provided an explicit link among our systems.

Pattern and frequency of disturbance to the research site. Our past and future efforts in this area are described in a major section of this proposal (p. 30).

2. LONG-TERM EXPERIMENTS

LTER participates in the Little Rock Lake Whole Lake Acidification experiment (p. 34). Following the acidification phase, a recovery experiment is planned which will test the hypothesis that recovery from a long-term stress is symmetrical to response to that stress. The recovery experiment is scheduled to start in April 1991 and funding for it is currently being sought. Other work on large-scale manipulations has involved an active collaboration with colleagues performing whole-lake experiments on food webs at the nearby University of Notre Dame Environmental Research Center. Our emphasis here, working with Steve Carpenter, has been improving techniques for interpreting whole-system experiments (Frost *et al.* 1988, Carpenter *et al.* 1989). Finally, we are continuing work on "natural experiments" tracking the long-term effects of species invasions (p. 30).

3. LONG-TERM DATA SETS

Our LTER program has developed an extensive series of long-term data sets derived from our ongoing measurements (Appendix Fig. 7, p. 74; Fig. 9, p. 76) at the NTL site as well as from historical data collected in the region (Table 9, p. 47). In several cases, detailed collections of remotely sensed data have been compiled using GIS technology.

4. DATA MANAGEMENT

Philosophy and Goals Data management has played a prominent role since the beginning of our LTER efforts and its importance has increased with the expanding temporal and spatial scales inherent in our continuing efforts. Our philosophy has been that data management is an integral part of the research process and our data systems have been designed to facilitate multidisciplinary investigations.

Three major goals characterize the design and implementation of our data management system: 1) maintaining database integrity, 2) providing access to researchers in a diversity of computing environments, and 3) facilitating linkages with diverse data sets (which may vary in observation period and variable types as well as ecosystem component measured). From the design of data collection through incorporation in centralized databases to analysis, our focus has been on the linkages among the diverse parts of the ecosystems we are studying.

Personnel. The data management staff consists of two half-time people. The data manager, Barbara Benson, is a Ph.D. ecologist and has been with the LTER project for six years; the programmer, Joyce Tynan, has been with LTER for four years. This length of service has provided substantial stability and continuity. The data manager is directly responsible to the lead P. I., and is also an active researcher on the project. Two other Ph. D. researchers (Carl Bowser and Tim Kratz) have substantial input to data management including design of data entry software, quality assurance, data flow, hardware and software acquisition and the general approach to research data management. Several technicians are responsible for data entry.

Data Sets and Availability. Core data sets collected by NTL and their status are summarized in Table 10, p. 48. Converting remaining non-computerized data to a computerized form is a high-priority goal.

Remote Sensing/Geographic Information Systems. Within the past few years, NTL researchers have added remote sensing and geographic information system technologies to our site's capabilities. We are beginning to integrate this activity into standard data management functions. One step has been developing linkages between the core databases and the RS/GIS software. An additional area of activity has been archiving and documenting GIS coverages and data derived from satellite image analyses. Further we are considering use of GIS applications for data management, such as: site management through identification of samples by geographic coordinates, and interactive data retrieval based on geographic coordinates.

Data Flow. Figure 29, p.49 depicts the flow of data from data entry at diverse locations to a centralized database on a mainframe at the central campus computing center. Retrievals from the databases then are provided in forms suitable to researchers operating in a heterogeneous microcomputing environment. Table 11 describes the primary hardware and software used by NTL researchers.

Documentation. We view documentation at several different levels as an integral part of research data management and as crucial to the long term usefulness of databases. Our experience in using the historical data sets from the Birge and Juday era has reinforced our commitment in this area (Bowser 1986). In addition to our general data catalog, each research program has an overall Research Study Abstract and a Variable Description Form and Code Form (Appendix Table 1, p. 79) for each data set included in the study. These forms have been completed for each computerized, core-data set and will be generated, as a matter of policy, for any LTER-related research.

Field and lab methods are documented for each data set. The data management staff maintains a protocol notebook containing schematic data flows, current programs, and statements of protocols such as database update procedures. Finally, a file is maintained showing a record of database updates.

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 further checked by ion balances, calculation of critical parameters from a redundant data set, and visual verification. Some error checking is built into the data entry software. Data entry is proofread by a two person team. Finally, summary tables are reviewed by researchers for errors.

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

Transferability to Other Sites. We regularly generate files containing summaries of each database. Such files can easily be transferred to other sites in ASCII form. We have responded to requests from researchers outside our project for data in electronic form and used the national networks to provide the data. Figure 30 illustrates our the connections to Internet and Bitnet.

Data Access. NTL centralized databases are maintained to assure data integrity. Access to primary files is limited to the data management staff. The SIR databases are password protected and reside on tapes with restricted access. Only derived data sets are used for analyses. These derived data sets are produced either by routine retrievals or through customized retrievals for special requests.

Table 12, p. 52 lists the requests for data by non-NTL scientists. These requests are channeled through the lead P.I., Magnuson, so that the relevant researchers at our site are aware of the request. Many of the data requests are met simply by sending a copy of existing summary tables. At other times, fulfilling the request entails a customized retrieval. In such cases, data are provided in an electronic form and can be sent via national networks.

Secure Storage. The SIR databases at the central campus computing center reside on 9 track magnetic tape. There are three copies, one of which is housed off-campus. Read access to these tapes is limited to the NTL group and write access is limited to the data management staff. A limited number of databases are maintained on the data management microcomputer and on back-up copies. In all cases, we also maintain paper copies of all data sets.

Long-Term Maintenance. We will continue to maintain multiple copies of our core databases on appropriate storage media, currently magnetic tape. In the coming year, we plan to change to a relational database management system (INGRES). Our currently used hierarchical system (SIR) is no longer state-of-the-art and no longer fully supported by the campus computing center. We will continue to balance the tradeoffs among continuity, startup costs, and the advantages of new software alternatives. As the NTL-LTER project evolves in the coming years, we will maintain our commitment to the documentation of methods and changes in methods, realizing how crucial such documentation will be for future uses of the NTL databases.

5. SYNTHESIS AND MODELING

Research at the North Temperate Lakes LTER is organized under the general synthetic theme of understanding ecological complexity that arises from the interaction of processes occurring at multiple temporal and spatial scales. Within this theme we have developed five areas of interrelated research (p. 2). The location of our site within a heterogeneous landscape of lakes, wetlands, and forests lends itself to spatial considerations ranging from a focus on a single lake to a consideration of groundwater flow patterns throughout the entire region. Likewise, our long-term data set allows us to examine seasonal, annual, and multi-annual dynamics. An alternative perspective involves differences in the focus of research within each of our conceptual themes. Examples range from assessments of the effects of global climate change on lake processes to evaluations of the interplay between nutrients and consumers in their influence on lake productivity.

Modelling efforts provide a common, synthetic thread that runs through our various research themes. Overall, our approach involves the use of several component models which may be computer simulation models, mathematical or statistical models, or conceptual models. We are not attempting to develop detailed simulation models for each of the components. Interaction among conceptual models, however, provide a synthetic context for individual studies at the site. Our use of models as synthetic tools enables us to integrate across multiple processes and bring together specialists from different disciplines.

Four examples developed in detail elsewhere in the proposal illustrate the synthetic nature of our modelling approach. 1) We are developing an extensive program to evaluate the effects of global climate change (p. 10). In this program we will couple physical and biological lake models (Fig. 31) to generate scenarios of the thermal and biological responses of lakes to altered climatic forcing. 2) Our proposed regional hydrologic model (p. 42) will link terrestrial, groundwater, and limnological processes, and will require cooperation among experts in forest ecology, groundwater flow modeling, isotope hydrology, and limnology. Ultimately, we plan to link this regional hydrologic model project with our efforts on global change. We expect to learn more about how our system operates now and how it may evolve under conditions of global climate warming. 3) Our investigations of the interplay between nutrient and consumer control of productivity in lakes (p. 23) requires cooperative expertise in groundwater hydrology and geochemistry, water chemistry, microbial ecology, and biological limnology. 4) Our assessments of variability patterns across the LTER network (p. 37, 54) illustrates synthetic cross-site comparisons of a fundamental characteristic of ecosystems. **6. INTERSITE AND NETWORK ACTIVITIES**

We expect that the development of general concepts and theory will be catalyzed by the overall LTER program and that our site can play an important role in this process. Clearly the terminology, taxonomy, and sampling systems that are appropriate for lakes are distinctly different than those used in terrestrial systems. Likewise, physical features and the timing of events in aquatic systems present major contrasts with forests, deserts, and grasslands. Despite these differences, general concepts in ecology must apply across terrestrial and aquatic systems. Our explicit attempts to include lake ecosystems along with terrestrial systems in overall LTER questions should help in the development of more general and robust ideas.

a. 1986-1990.

One major contribution in our intersite research during the last five years was to organize and lead a comparative study of ecosystem variability. In this research, funded by the LTER Network and North Temperate Lakes LTER grants, we developed a metric for spatial and temporal variability of ecosystems which was neither parameter nor ecosystem specific. Using this metric we compared the variability patterns across 12 LTER sites. In the process we also generated the first public LTER-intersite database "VARNAE," on deposit at the LTER Network Office in Seattle (documentation in Appendix Table 3, p. 86). Magnuson visited most of the 12 participating sites to discuss our approach and to seek their participation. Kratz developed the database. North Temperate Lakes investigators hosted an analysis-based workshop at the Trout Lake Station in April 1988 which resulted in a series of publications (Magnuson *et al.* 1990, Kratz *et al.* in review, Kratz *et al.* manuscript). See page 37 for additional details on results.

Representatives from our site have participated in a variety of additional intersite activities (Table 13).

In addition to these activities, Magnuson has been a member of the LTER Steering Committee, the LTER Network Executive Committee since its inception, and was an assistant to the editor of the LTER newsletter "LTER NETWORK NEWS" during its formative years. He also helped to develop the Strategic Planning Exercise in October 1989.

b. Proposed Intersite Activities

We will continue to be an active participant in intersite activities. We are planning to host three major, research-oriented meetings in the next several years. Each of these meetings will be modeled on the successful format of our variability workshop. The meetings will be science and product oriented and will include representatives of both LTER and non-LTER sites. We will also participate in the six projects summarized in a separate document as LTER Cohort 1 intersite research.

Spatial Analysis. We will continue to provide leadership in developing the intersite use of remote sensing RS/GIS technologies. We propose to organize an intersite research workshop to compare the structure of the divergent landscapes represented in the LTER network from the perspective of the influence of grain and extent on the spatial heterogeneity of landscapes. We would use data from Landsat, SPOT and selected AVHRR scenes for 1990 which are being purchased by the LTER network office. We will draw heavily on our site's expertise on RS/GIS technologies to lead this effort. Our Environmental Remote Sensing Center, within the Institute for Environmental Studies has the computer facilities and personnel to host the workshop.

Comparative Hydrology. We propose to organize a workshop on comparative hydrology of the LTER sites to compare approaches and to develop common means of defining the hydrology of each site as it relates to broader LTER research objectives. Understanding the hydrologic regime and its effect on material transport is an important goal for all LTER sites. One organizing theme involves the question, To what extent is hydrologic regime coupled to the movement of materials across landscapes?

Comparative Long-Term Limnology. We also are planning a large scale, interactive symposium on long-term ecological research on lakes. This symposium will be preceded by a smaller workshop in which appropriate analytical approaches and data formats are developed to facilitate interactions at the symposium. We are particularly interested in examining 1) long-term temporal variability in lakes and 2) patterns of variability among lakes within geographical areas of varied sizes. The symposium will draw from an international group of investigators with access to extensive data bases, including researchers from LTER sites.

Other: In addition to these major activities we will be active participants in intersite activities including many organized by other sites. One example is the long-term decomposition experiment organized by Mark Harmon of Andrews. Other projects are in preliminary planning stages, including climate change effects on site hydrology at various spatial scales, plant demography across LTER sites and Allen's comparisons of system turnover rates.

7. RELATED RESEARCH PROJECTS

The NTL-LTER site has a general policy to encourage the development of collaborative programs with outside investigators. These programs vary in the strength of their relationship to LTER, but all benefit and are benefited by the LTER project. Twenty-five collaborative projects are currently underway (Table 14).

8. ARCHIVES AND INVENTORIES

Historic data. Early in the project we produced a detailed inventory of the available historic data from the Trout Lake site. The earliest and most complete aquatic data were collected by E.A. Birge, C. Juday, and their colleagues from 1924 through 1942 (Frey 1963). The extent and scope of their work is impressive, spanning more than 500 lakes in the Northern Highlands Lake District and covering numerous of physical, chemical, and biological parameters. We also have an excellent long term data base for Lake Mendota with ice duration data beginning in 1852. Major portions of the water chemistry, phytoplankton, and zooplankton data have been computerized by various agencies or our project researchers. For Chemistry see Eilers *et al*. (1989), for weather and physical limnology see Robertson (1989). The historical data are described in Lehner (1980) and Lehner *et al.* (1980); these papers include an index to the holdings of original data in the University archives. In addition we have gathered historic maps and documents relevant to the site which are now available at the Trout Lake Station and the Laboratory of Limnology. Some of our uses of these data are described above in regard to zooplankton (page 37) and physical limnology and weather records (page 6).

Samples. The first ten years of the North Temperate Lakes LTER project has generated a variety of physical samples which are housed at the Zoological Museum or, on a temporary basis, at the Trout Lake Station, the Laboratory of Limnology, or the Geochemical Laboratory. These include annual collections of frozen, dried or preserved specimens. Details on collections of fish, invertebrates, plants, water samples and phytoplankton are listed in Table 15. In addition, we have developed reference collections of fishes, unionids, decapod crustaceans and macrophytes. We have a regional collection, cataloged in the Zoological Museum, of fishes from small seepage lakes made by Frank Rahel and John Lyons. Through cooperation with Frederic Harrison we plan to repeat the survey of the freshwater sponges made by Minna Jewel during the Birge and Juday era and to prepare a reference collection. We have made a concerted effort in this area because we fear that, at our site and at others, adequate attention is paid only infrequently to the permanent archiving of materials.

9. LEADERSHIP, MANAGEMENT, AND ORGANIZATION

In general, the Program Director (John J. Magnuson) with the assistance of the Deputy Director (Carl J. Bowser) have overall responsibility for program management and direction. Major scientific input on research goals and policy is provided by the principal investigators. The Site Manager (Timothy K. Kratz) oversees regular sampling and supervises field technicians. The Data Manager (Barbara J. Benson) develops the data management system with Bowser, and is responsible for the reduction, storage, and retrieval of data; she also supervises a part-time museum curator, a programmer and hourly help. Bowser supervises the chemistry laboratory. Support Staff at the Center for Limnology assist the Director with fiscal, personnel, and clerical activities. Technicians conduct most field work and sample processing. Research is planned and implemented by a diverse group of principal investigators, research scientists and graduate students. Personnel and bibliographic information for our PI's are provided in Appendix H, p. 105.

10. NEW PROJECTS AND TECHNOLOGIES

Local Area Networks and Wide Area Networks. We have connected LTER related computer facilities to local area networks at the Environmental Remote Sensing Center and the Limnology Laboratory. Computer at both facilities are also connected to the UW-Madison Campus Area Network via an Ethernet line providing access to various wide area networks including INTERNET and BITNET. These networks have facilitated 1) data transfer between cooperating departments on the UW-Madison campus and the Trout Lake Station, 2) data transfer to other LTER sites and cooperating researchers, and 3) our access of EMail through various networks including the LTER bulletin board.

Remote Sensing and GIS. Through NSF supplemental funding, we have acquired a COMPAQ 386/25 MHz microcomputer based remote sensing/geographic information system (RS/GIS). Both ARC/INFO (a vector based GIS package) and ERDAS (a raster based image processing and GIS package) have been installed on the COMPAQ. We have developed methods of integrating both packages through the ERDAS LIVE-LINK for which our remote sensing center served as a beta test site (Appendix Fig. 8, p. 75). This product has been developed by ERDAS and ESRI and allows for ARC/INFO vector data to be interactively entered over an ERDAS raster image. This product represents one step towards full integration of raster and vector formats and we have been investigating ways to utilize this integration. We are constantly developing new algorithms and software for remote sensing and GIS (Bucheim and Lillesand 1989, MacKenzie *et al.* In Press).

As part of a practicum course being taught by Tom Lillesand and colleagues at ERSC, 11 graduate students developed and demonstrated a combined RS/GIS for NTL-LTER (Lillesand *et al*. 1989, Morrison and Ribanszky 1989). Specific demonstration projects included 1) documenting the nature of land cover changes from the presettlement period of the 1830's to present (Appendix Fig. 5, p. 72 top), 2) investigating soil/pre-settlement vegetation associations, 3) developing lake level change change scenarios in response to global climate variations, 4) modeling the spatial distribution of groundwater parameters, 5) evaluating geometric error inherent in map digitizing, and 6) assessing intra- and inter-lake water quality variability on a regional basis using Landsat Thematic Mapper T data. Other output from the workshop are in Appendix Fig. 1, p. 68 top left; Appendix Fig. 5, p. 72; and Appendix Fig. 8, p. 75).

11. DISSEMINATION OF INFORMATION

We have published scientific papers, presented papers at scientific and professional society meetings; written popular articles; organized sessions on long-term ecological research at scientific and professional meetings; lectured at universities, civic clubs and agencies; participated in briefings to NSF and other agencies; conducted a remote sensing and GIS practicum for graduate students; taken limnology laboratory classes to the LTER site for their class projects; incorporated LTER research findings into our lecture classes; provided original and summary data to inquiring parties; and worked on the LTER newsletter.

IV. SUPPORTING MATERIALS

A. SITE DESCRIPTION

The rich history of pioneering limnological work at Trout Lake and the strong tenor of current research activity combine with an ideal location to make the Trout Lake Station uniquely suited as a center for aquatic field studies. The Northern Highland Lake District, with an area of approximately 10,000 km2, has one of the highest concentrations of lakes in the world. Within Vilas County alone, where the Trout Lake Station is located, there are over 1300 lakes, covering 16% of the surface area. Within a 10 km radius of the station there are 68 named and 38 unnamed lakes (Fig. 20, p. 30). The range of limnological conditions within the district is remarkable. Lakes range in size from 0.1 to over 1500 ha, in depth from 1 to 33 m, and in fertility from oligotrophic to eutrophic. Other representative limnological conditions include: groundwater dominated and drainage lakes; lakes with varved sediments, winterkill lakes, temporary and permanent forest ponds, and reservoirs. Lakes are influenced by strong seasonality and are usually ice covered from late November to late April. The district is also the source area for several major river systems. The county surrounding the station has approximately 640 km of permanent streams and numerous intermittent streams.

Lakes within the Northern Highland exhibit near natural water quality conditions (Appendix Fig. 1, p. 68; Fig. 2, p. 69; Fig. 3, p. 70; Fig. 4, p. 71; and Fig. 6, p. 72). Near the Trout Lake Station, the lake district lies within the Northern Highland and American Legion State Forests, which protect 80% of the land area and about two-thirds of the lake frontage. Many lakes have totally forested watersheds and no private frontage. There is no heavy industry and only a sparse population density in the area. Detailed investigations have indicated minimal effects of acid deposition on lakes in the region to date. Outdoor recreation and forestry form the economic base for local communities.

Climate in the region is cool with a growing season of about 195 frost-free days. The average annual temperature is less than 5¡C. The area receives approximately 76 cm of precipitation, about 30% of which falls in spring, with June and following summer months being the rainiest. This area receives 127-152 cm of snow which covers the ground for about 120 days each year.

Several existing data bases and projects also contribute to make the site unique. The pioneering work of Birge and Juday provides a more extensive body of information for northern Wisconsin lakes than exists for any other region. Similarly, the whole-lake experimental work of A. D. Hasler has created an enduring archive of limnological evidence. During the 1950's, a number of lakes in the district were manipulated by liming, phosphate addition, piscivore removal, or addition and removal of planktivores. Chemical and biological responses to these treatments were documented during the experimental work and the results are partially stored in the sediment record. The value of the experimental approach practiced several decades ago is enhanced by current paleolimnological approaches coupled with mechanistic understanding (Kitchell and Kitchell 1980). Contemporary and future work can profit from the paleolimnological evidence of immediate and long-term responses to large-scale manipulation.

Research activities at the Trout Lake Station are extensive. Also, the Station is within 15 km of the Wisconsin Department of Natural Resources' major warm water

fish research site, the Five Lakes Experimental Fisheries Area, which has been collecting fisheries data continuously since 1946. Finally, the Trout Lake Station lies in close proximity to the University of Notre Dame's Environmental Research Center. Numerous activities at the two facilities are conducted in close collaboration. Together the Trout Lake Station and the Notre Dame Center form a site within the Experimental Ecological Reserve Program. These facilities combined with a third location in the upper peninsula of Michigan will be included in the Biosphere Reserve System of the UNESCO Man and the Biosphere Program.

B. THE CENTER FOR LIMNOLOGY

Our NTL-LTER program is operated by the Center for Limnology at the University of Wisconsin, Madison. The Trout Lake Station is one of two laboratories composing the Center; the other is the Limnology Laboratory on Lake

Mendota. The Center functions administratively with a Director, (John J. Magnuson), Associate Directors for the Trout Lake Station (Thomas M. Frost), the Madison Lakes (Stephen R. Carpenter), and the Limnology Laboratory on Lake Mendota (James F. Kitchell), a Research Program Manager, a Laboratory Manager, a Data Manager, a Librarian, an Instrument Maker and a Secretarial Staff of three. Oversite and planning for Center activities is provided by the Center's Faculty Advisory Committee, appointed by the Dean of the College of Letters and Science.

Support of the Center includes an operating budget (FY90) of $343,580, extramural funding (FY90) of $1,180,157, Graduate School support from the Wisconsin Alumni Research Foundation of $25,000/yr., a $644,945 endowment, and capital equipment support from the University sources of $45,000/year. Details on University support for LTER facilities and equipment is presented in Supporting Materials D. p65-66. The Trout Lake Station serves as a field site for many of the Center's research programs including LTER. Other University of Wisconsin facilities that support LTER include the Limnological Laboratory on Lake Mendota, the Geochemistry Laboratory of the Department of Geology and Geophysics, the Water Chemistry Laboratory, the University of Wisconsin Zoological Museum, and the Madison Area Computing Center.

C. FACILITIES

Trout Lake Station (Appendix Fig. 11, p. 77) consists of a complex of buildings located on the shore of Trout Lake. Most buildings are operated year-round and include a main laboratory, residence facilities, and several service buildings. Although the actual physical property of the station is only 20 ha, we provide ready access to the numerous lakes of the Northern Highlands district.

Our all-season laboratory is a two story structure with more than 7,500 ft2 of space located about 35m from the shore of Trout Lake. The upper floor contains a chemistry laboratory and five research laboratories, which are equipped with gas, natural and heated well water, compressed air, electricity and water from Trout Lake. One laboratory is designed for super-clean conditions necessary for trace metal sample processing. The upper floor also contains a library conference room, eight offices, a lunch room and a computer room. The lower floor of the station provides space for field gear storage, sample processing, aquarium facilities, and a primary production incubation lab. Light and temperature conditions can be controlled in the three aquarium and incubation rooms. Specialized laboratories are available for microscopy, high performance liquid chromatography, and radio-isotope work. Critical equipment at the laboratory is serviced by an auxiliary power plant. Five service buildings at the station provide facilities for equipment and vehicle storage.

Year-round housing at the station currently provides space for 22 people. During the period from May until October, non-winterized cabins provide an additional 12 spaces. Construction is currently underway on an additional year-round cabin, which in conjunction with a second new cabin planned in 1991, will yield a total capacity of 30 in winter and 45 during the rest of the year. Housing at the station is provided only for short-term stays (<1 year). Permanent resident employees provide their own housing offstation.

Trout Lake Station is well equipped to provide access for researchers to nearly any aquatic site in the lake district. Major field gear includes: three four-wheel-drive trucks, three large and two small boat trailers, a ski barge, five Arkansas traveler workboats, seven alumacraft rowboats, five outboard motors, and two canoes. A snowmobile, ice drills, snowshoes, and insulated field boxes are available for winter limnology. Scuba gear is also available. We have most standard collecting gear for general limnological work including masterflex peristoltic pumps with in-line filtration, meters and probes to measure light (PAR and full spectral characteristics), temperature and oxygen *in situ*, plankton samplers, trawls, fyke nets, gill nets, seines and both large and small electroshocking boats.

Our laboratories are equipped with fume hoods, a millipore reverse-osmosis and milli-Q water purification system, drying ovens, muffle furnace, dry sterilizers, balances (in a variety of ranges including a Cahn Electrobalance, pH meters, recorders, a Waters High Performance Liquid Chromatograph with a diode array detector, a Kontron Double-Beam Spectrophotometer, fluorometer, and a Beckman model LS 1801 liquid scintillation counter. A set of five, light-and temperature-controlled incubators are available for experimental projects and culture maintenance. In addition, a wide variety of analytical equipment is available at several facilities on the Madison campus. Microscopes available at Trout Lake include: a Zeiss Inverted Microscope equipped for epifluorescence, a Nikon

Labophot microscope, and 3 Wild model M5A dissecting scopes. The laboratory has a series of large fiberglass holding tanks, four 75-gallon fiberglass aquaria and assorted small aquaria. Portable generators and pumps allow the use of holding tanks at remote sites throughout the region. Detailed meteorological data are currently recorded at a nearby land-based station and on a fully-instrumented raft currently operated on Sparkling Lake (3 km from the station). Chemical precipitation data are available from an NADP site located at Trout Lake and serviced in our laboratory.

Laboratory of Limnology. The Laboratory of Limnology (Appendix Fig. 11, p. 77) on the Madison campus serves as the administrative base for NTL- LTER and the Trout Lake Station. It is also a field station for Lake Mendota research. Primary LTER data management activities are conducted here.

Geochemistry Laboratory. Chemical analyses for lake and groundwater monitoring are performed in the geochemistry laboratory in the Department of Geology and Geophysics on campus in Madison. Analyses are conducted by a full-time specialist with the assistance of hourly helpers. Analyses, data reduction and logging, preparation of reagents, standards, and ultra-clean sampling bottles, and the oversight of supply needs for both the geochemistry laboratory and the Trout Lake chemistry laboratory are all part of the specialist's responsibilities.

Water Chemistry Laboratory. The Water Chemistry Laboratory, located in the Water Science and Engineering Laboratory adjacent to the Limnology Laboratory also serves as a second center for research on biogeochemical cycling in LTER lakes. Laboratories are well equipped for both applied and basic research on analytical chemistry, chemical speciation, geochemistry, the chemistry of particle surfaces, and the chemical properties and partitioning of organic compounds. Field equipment for detailed sampling of water, sediments and air is available.

Zoological Museum. We use the museum, directed by John A.W. Kirsch, Professor of Zoology, for curation of our growing collections of limnological materials primarily fish, invertebrates, and plankton. The museum is also the repository for remaining samples from the Birge and Juday era. The Zoological Museum provides a safe and professional repository for long-term research collections for aquatic ecology and limnology.

Computing Facilities. NTL-LTER researchers are using microcomputers at several different locations on the Madison campus and at the Trout Lake Station. At the Center for Limnology ten Macintosh computers are connected via an APPLEtalk network and TOPS software is installed on six of these. In addition, there are two IBM compatibles and two Apple IIe. At Trout Lake, there are 9 computers used by LTER researchers (six Macintosh, three IBM's). At the Geochemistry lab, there is one Macintosh II connected to a local area net and two Apple IIe's.

NTL-LTER has a 386/25 PC-based GIS workstation located at the Environmental Remote Sensing Center on the Madison campus. The software for this machine includes all six available pcARC/INFO modules and ERDAS version 7.3.

The University of Wisconsin-Madison has a campus-wide network, the Wisconsin IPNetwork which is a broadband ethernet. The LAN's at the Center for Limnology, at Geology/Geophysics and the Environmental Remote Sensing Center are connected to the campus network.

We also use the VAX cluster (VAX-8650, two VAX 6310) at the Madison Area Computing Center (the central campus computing facility).

Environmental Remote Sensing Center (ERSC) ERSC researchers have developed an extensive set of resources for digital image processing. These include various commercially available (ERDAS, McIDAS) and in house developed software packages for analysis of digital satellite (Landsat, SPOT, AVHRR, GOES, and Meteosat) data, digitized photography, and electro-optical scanner data. ERSC researchers also make extensive use of geographic information system (GIS) resources including the ARC/INFO, ERDAS, EPPL7, and pMAP software packages. ERSC computing is supported by a local area network which includes: 1) four research image processing and GIS workstations (two of which are built around 80386/25 MHz CPUs), 2) 6250 tape drive, 3) two, 200 MB optical disk drives, 4) 35 mm film recorder, 5) various printers and plotters, 6) scanning/writing microdensitometer, 7) modems, and 8) a link to the UW-Madison Campus Area Network with its access to INTERNET and BITNET. A recent instructional lab modernization grant from the

University will allow ERSC to establish an instructional lab with nine ERDAS, ARC/INFO workstations and ancillary peripherals.

ERSC maintains equipment for data acquisition: 1) a Barnes PRT-5 and a Barnes Modular Multiband Radiometer (MMR) for multispectral field measurements, 2) 35mm, 70mm, and 240mm camera systems for aerial photography, and 3) a Texas Instruments thermal scanner.

ERSC maintains equipment for visual image analysis: 1) a full range of pocket, mirrored, scanning, and zoom stereoscopes, 2) a zoom transfer scope, 3) a color additive viewer, and 4) supporting photographic darkroom equipment.

D. UNIVERSITY SUPPORT AND SUPPORT STATEMENT

1. University Contributions for Long Term Ecological Research

The University of Wisconsin-Madison provides significant and sustained support for the Long Term Ecological Research program underway at the Center for Limnology. Beginning in 1980 with an LTER start up award of $21,800 from the UW Graduate School, the University has continued to provide personnel support, supplies and capital and facility improvements to enhance LTER research. The College of Letters and Science provides a current Center operating budget of $343,580 including personnel, travel, supply and service funds. Starting in 1982 the Graduate School provided five years of development funding for the Center in the amount of $150,000.

Personnel: In recognition of increased activities the Center's College of Letters and Science has provided an additional 2.9 FTEs for the annual operating budget of the Center during the 1980's. The most significant addition to personnel was the creation and funding of a permanent, full time Associate Director at the Trout Lake Station, field site for the northern lakes LTER program. This position is currently held by Thomas Frost, a co-investigator for LTER. Other personnel additions include a librarian, aquarium facility manager, and custodial and secretarial support.

Support for a third faculty member derived from the Center's Endowment (see below), the Bassett Foundation, the Graduate School and the College of Letters and Science has resulted in the Center appointment of Dr. Stephen Carpenter as the first Bassett Professor of the Madison Lakes. Dr. Carpenter joined the Center staff this fall and provides additional faculty strength for Center programs including LTER.

The Graduate School provides funds to support the Center's undergraduate, work-study assistants, many of whom work on LTER. This funding not only supports workers for LTER research it also provides invaluable experience for undergraduates interested in multi-disciplinary aquatic research. In addition the Graduate School has provided faculty summer support and graduate student support in the form of Fellowships. Graduate student support averages $15,000/yr.

Facility Improvements: The decade of the eighties has seen significant facility improvement for the Center. At the Center's Trout Lake Station a housing unit was completed and dedicated in 1982. The Juday House now provides housing for LTER investigators. Funding for this unit was provided by State building funds ($31,250) and the National Science Foundation ($47,250). In 1985 funds were approved for construction of a main laboratory addition of 2,400 square feet, increasing the laboratory area to 6,069 square feet. Funds for this addition were provided by the UW Graduate School ($40,000), College of Letters and Science ($40,000) and the National Science Foundation ($165,000). The Graduate School provided $30,000 for movable equipment for this laboratory addition.

In addition to the above, the College of Letters and Science has provided the Center's Trout Lake Station with three additional housing units ($86,812), water supply improvements ($8,400), Juday House basement apartment additions ($11,500) and has funded the burying of power lines to the site ($8,400).

In Madison the Center's Laboratory of Limnology facility improvements supporting LTER include a new library ($34,400), a new computing facility ($9,000) and a remodeling of the wet lab staging area ($25,000). In addition, all campus support in the amount of 1.8 million dollars for remodeling of the Hydraulics Building into the recently completed Water Sciences Laboratory has provided the Center with a state of the art experimental aquarium and wet lab facility of 2,000 square feet. A grant of $496,000 from the Department of Education has provided moveable equipment and furniture for this facility.

Space and facilities for analysis of LTER chemical parameters is provided by the College of Letters and Science department of Geology and Geophysics under the direction of Co-Investigator Carl Bowser.

Capital Equipment: Funds for capital equipment specific to LTER needs are provided to Campus LTER investigators from the Colleges of Letters and Science, Engineering and Agriculture and Life Science as well as the Institute for Environmental Studies and the Graduate School. Funds for these capital improvements in support of LTER have provided for an HPLC, Auto Analyzer and enhanced computing facilities. Capital acquisitions for the Center programs average $45,000/year. From this source, funding for LTER capital needs over the decade are estimated at $25,000/year.

Endowment: Following establishment of the Center as an independent research unit in 1982, the Center's College of Letters and Science and the University of Wisconsin Foundation initiated a Center for Limnology Endowment. To date Development Directors from the College and Foundation in concert with Center staff have raised $644,945 segregated into seven functional areas:

1. General Endowment $42,990

2. Anna Grant Birge Memorial Scholarship Fund $70,981

3.Dorothy Powers Grant and Eugene Lodewick

Grant Scholarship Fund $20,000

4. Chancey Juday Limnological Data Fund $19,450

5. Chase Noland Scholarship in Limnology $17,760

6. Donald Halverson Limnology Fund $462,842

7. William V. Kaeser Visiting Scholar Fund $10,922

Recipients of support from these seven funds include LTER investigators and students, both graduates and undergraduates.

2. Support Letter from Chancellor Shalala

E. APPENDIX FIGURE LEGENDS

Appendix Figure 1. Perspectives of the NTL LTER study site over multiple spatial scales. (**UPPER LEFT**) June 9, 1988 Landsat 5 TM imagery of the Trout Lake region, (**UPPER RIGHT**) Aerial photo of Sparkling Lake ecosystem, (**LOWER LEFT**) Sparkling Lake littoral community. (**LOWER RIGHT**) individual and population biology.

Appendix Figure 2. NHAP high altitude aerial photograph of the Trout Lake area taken May 8, 1983. Trout Lake is the large lake in the center of the photograph.

Appendix Figure 3. View of mesotrophic Trout Lake from the Trout Lake Station.

Appendix Figure 4. (**TOP)** Dystrophic bog lake, and (**BOTTOM**) oligotrophic Crystal Lake. Crystal is a popular camping and swimming site owing to sandy beaches and clear water.

Appendix Figure 5. (**TOP**) Land cover map of the Trout Lake area derived from June 9, 1988 Landsat 5 TM imagery. Land cover types were identified using a supervised classification. Data reside in a raster GIS file with 30m pixel resolution (after Morrison and Ribanszky 1989). (**BOTTOM**) Soil texture of the Trout Lake area derived from vector GIS file of soil map units. Soil map units were digitized from the USDA SCS Soil Survey of Vilas County (after Morrison and Ribanszky 1989).

Appendix Figure 6. Oligotrophic, clearwater lake showing the allochthonous inputs of leaves and coarse woody debris and the emergent macrophytes in the littoral zone.

Appendix Figure 7. Collecting water column samples for primary productivity analysis in Little Rock Lake, the secondary lake being used for the experimental acidification.

Appendix Figure 8. (**TOP**) Turbidity map for lakes of the Trout Lake region. Data derived from regression analysis of June 9, 1988 Landsat 5 TM imagery and near concurrent "ground" truth data (after Morrison and Ribanszky 1989). (**BOTTOM**) Contour and bathymetry information for Trout and Allequash Lakes. Contour and bathymetry information were digitized from the USGS 7.5" quadrangle map. This figure illustrates the integration of vector GIS data (the contour and bathymetry data) with raster data (the background image displaying TM bands 4,5,3).

Appendix Figure 9. Winter sampling. (**TOP**) Snowmobile and equipment sled take researchers to lake sampling site on the ice of Trout Lake. (**BOTTOM**) Zooplankton sampling with a Schindler-Patalas trap on one of the LTER dystrophic lakes.

Appendix Figure 10. Depth versus date limnological profiles for Trout Lake from January through December 1987. Variables are water temp (red), oxygen concentration (green), oxygen saturation (blue), and a color composite of all three variables. Bright colors represent high values, dark colors represent low values. All variables are stored in a raster GIS file. The color composite illustrates the utility of digital image processing techniques in displaying three variables simultaneously. The data for this figure were all derived from the NTL-LTER core data set (after MacKenzie *et al*. in press)

Appendix Figure 11. The Center for Limnology's two field laboratories: (**TOP**) The Laboratory of Limnology on Lake Mendota - University of Wisconsin's Madison campus. (**BOTTOM**) The Trout Lake Station on Trout Lake in the Northern Highlands Lake District of northern Wisconsin.

F. APPENDIX TABLES AND DOCUMENTS

- 1. Appendix Table 1. North Temperate Lakes data documentation forms. A Research Study Abstract is completed by each research study and a Variable Description Form and Code Form are completed for each data set included in the study.Appendix Table 3.

Documentation for VARNAE an LTER intersite database on variability in North

American ecosystems

APPENDIX Table 3.

DOCUMENTATION FOR "VARNIE", AN LTER INTERSITE DATABASE ON VARIABILITY IN NORTH AMERICAN ECOSYSTEMS

Prepared by

Tim Kratz - North Temperate Lakes

13 June 1988

This document describes the LTER Intersite data set on variability in North American ecosystems. The dataset, VARNAE, was created during the winter of 1988 and was the focus of a workshop held at the Trout Lake Station, Wisconsin on 18-21 April. VARNAE is the first public LTER Intersite Database and it is on file at the network office in Seattle. The goal of the workshop was to examine patterns of temporal and spatial variability in ecological parameters across diverse types of North American ecosystems, focusing on time scales of years and spatial scales of landscapes. The workshop was, perhaps, the first LTER workshop where the primary goal was to analyze intersite data and answer research questions.

Each participating site created a series of data matrices, one for each parameter, from which various statistics were computed for inclusion in VARNAE. Each matrix contained values representing the value of the parameter for a given year in a given location within the LTER site. From these "raw" data matrices two types of files were created: location detail files, and a summary file.

VARNAE consists of the following items.

- 1. A series of "location detail" files.
- 2. A summary data file.
- 3. A data dictionary.
- 4. This documentation.

Location Detail Files.

Location detail files contain data summarizing the behavior of each parameter in each location, averaged across years. Each record in a location detail file consists of at least 7 fields: a location identifier (i.e. which watershed, lake, plot, or other sampling site within an LTER site), a parameter identifier, the average value of the parameter over the years of record, the standard deviation about the mean, the coefficient of variation, the number of years of record, and the range. VARNIE contains 32 separate location detail files with information on a total of 489 parameters.

The Summary Data File.

The summary data file contains summary statistics for each of the data matrices described above. The file contains 489 records; each record contains 43 fields with information about a single parameter from a single LTER site. The fields are:

Field No. Field Name Field Description

- 1 SITE The LTER site

  2 FULL DESCRIPTION Brief description of the parameter

3 UNITS Units of measurement

4 VAR Short name for parameter

5 NLOCS Number of locations within LTER site

6 NYEARS Number of years of measurement

7 STARTYEAR The starting year

8 ENDYEAR The ending year

9-18 TYPE1-TYPE10 Descriptors (see data dictionary)

19 MEAN Grand mean for parameter

20 STDEV Standard deviation about grand mean

21 N Number of data points in matrix

22 SSTOT Total sums of squares from 2 way anova

23 SSLOC Sums of squares for location effect

24 SSYEAR Sums of squares for year effect

25 SSOTHER Sums of squares for error and interaction

26-28 R2's MOD2 r2 due to year, location and other from

Model II Anova

29-31 R2'S MOD1 r2 due to year, location and other from

Model I Anova

32-34 MS's Mean squares for year, location, and other

from two-way ANOVA on raw data

35-37 SIGRAW'S Variance due to year, location, and other

based on 2-way ANOVA on raw data

38-40 SIGREL'S Variance due to year, location, and other

based on 2-way ANOVA on relativized data

41-43 MS (/MEAN'S) Mean squares for year, location, and other from two-way ANOVA on relativized data

- The details of calculation of fields 22-43 follows.

Fields 22-43 result from a standard two-way analysis of variance where location and year are the two treatment effects. Because there is only one value of a parameter for each location-year combination, there is no replication and the effects of interaction and error cannot be separated. We have lumped interaction and error together in a category called "other". The two-way analysis of variance was conducted on both the "raw data" as supplied by each LTER site, and also on "relativized data". Data were relativized by dividing each value in a location-year matrix by the grand mean for that matrix. This relativization was done to dampen the effects of measuring different parameters with different units, and thus, make comparisons among different parameter types easier. We used only matrices that had no missing data. The values given in fields 22-25 are the sums of squares obtained using the "raw data".

Mean squares from the two-way anova are given in fields 32-34 (for the raw data) and 41-43 (for the relativized data). These means squares are, of course, simply the appropriate sums of squares divided by the degrees of freedom minus 1.

The magnitude of variation owing to location, year, and other were computed for both the raw and relativized data using the expected values for a two-way analysis of variance.

Treatment Expected Mean Square

location s2 + nyears * s2loc

year s2 + nlocations * s2year

other s2

Therefore, we computed s2loc, s2year, and s2 from the following formulas:

s2loc = (MSloc - MSother)/nyears

s2year = (MSyear-MSother)/nlocations

and s2 = MSother.

By convention, negative values of s2loc or s2year have been set to zero.

These values are named, for example, "SIGYEARRAW" if it was computed from the "raw" data (fields 35-37), and "SIGYEARREL" if it was computed from the relativized data (fields 38-40).

We computed the proportion of variance explained by location, year and other in two ways: from a Model I Anova, and from a Model II Anova. We think the Model II analysis is more appropriate and recommend using the Model II values. Model I r2's are computed from the sums of squares as follows:

r2location = ssloc/sstot

The model I r2's for year and other are computed similarly (fields 29-31).

The model II r2's were computed as follows:

r2location = s2loc/(s2loc + s2year + s2other).

and similarly for year and other (fields 26-28).

Note that for the r2's equivalent values are obtained by using either the raw or the relativized numbers.

The Data Dictionary

The data dictionary consists of a subset of fields from the summary data file and serves to describe attributes of each variable (e.g. plant, animal, etc.). The first page of the data dictionary and a legend for abbreviations used in types 1-9 are included as an attachment to this document. While the data dictionary gives some details about each parameter, it is not meant to be a complete guide. Questions about individual parameters should be addressed to the appropriate LTER site.

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