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I. INTRODUCTION

We propose to continue our long-term ecological research program on temperate lakes (Magnuson et al. 1984) in the Northern Highland Lake District of Wisconsin as part of an interactive national program of Long Term Ecological Research (LTER) on 11 sites across the United States (Halfpenny and Ingraham 1984).

Our proposed research is focused on extended temporal and spatial scales. In examining annual patterns in lakes we emphasize year-to-year variability and the implications of such variability for community and ecosystem processes. We consider a suite of lakes within close proximity to each other that differ dramatically in physical, chemical, and biological characteristics but that share a common climate and edaphic conditions. Our approach is geared to time scales and dynamics that are associated with long-term changes in the structure and function of ecosystems.

Lakes provide ideal systems for long-term ecological research. Their boundaries are relatively distinct, and adjacent lakes, while similar to each other in one sense, may differ greatly in physical, chemical, and biological properties and processes. Thus, a set of lakes can be used in natural experiments to at least partially isolate important control factors external to and within the lake. Clarity of the boundaries makes lake sites especially useful for analysis of landscape scale processes. A long tradition of limnological work has laid a substantial groundwork for our research. Important ecological variables have been identified and information is available to suggest measurement frequencies that will minimize interferences from short-term variations. A substantial amount of early limnological research in North America was conducted on our LTER lakes by Birge, Juday and their colleagues in the first half of this century (Frey 1963).

Because lake ecosystems superficially appear quite different from the principal ecosystems at the other LTER sites, i.e. forest, prairie, desert, tundra, saltmarsh, and river; the northern lakes also provide an ideal system from which to explore, develop, and test ecological theory at the intersite level. To include lakes in intersite research, we must operate at a very general level. Ultimately, ideas generated in this way will apply to a more diverse group of ecosystems than would theory developed for a single more narrow range of ecosystems.

The LTER site on north temperate lakes operates on the following major objectives and principles:

1) To perceive and describe long-term trends and patterns in physical, chemical, and biological properties of lake ecosystems
2) To understand the dynamics of internal and external processes affecting lake ecosystems
3) To analyze the temporal responses of lake ecosystems to disturbance and stress
4) To evaluate the interaction between spatial heterogeneity and temporal variability of lake ecosystems
5) To develop and test concepts and theories relating temporal and spatial variability of lake ecosystems at scales relevant to long-term landscape ecology

The last two objectives are new and have grown out of our research in years 1-5 and a desire to search for generality both at the site and the intersite levels. Specific research questions we developed five years ago are listed in Appendix 2. A revised set of questions are developed in the body of this proposal under each major objective.

In our first 5 years we recognized that until long-term data sets were available, we must develop approaches in initiating long-term ecological research on lake ecosystems using basic concepts and short-term data. Our approaches, in addition to initiating our long-term measurements, were to compare recent LTER data (1979-1984) with similar historic data collected during the Birge and Juday era on northern Wisconsin lakes (1925-1942), to evaluate interyear variability within and among lakes with historic and recent data, and to develop an understanding of the principal external and internal linkages affecting the dynamics of the LTER lakes.

II. RESEARCH PROGRESS AND PROPOSED RESEARCH

A. INTRODUCTION

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

B. PERCEPTION AND DESCRIPTION OF LONG-TERM TRENDS AND PATTERNS IN PHYSICAL, CHEMICAL, AND BIOLOGICAL PROPERTIES OF LAKE ECOSYSTEMS

1. ESTABLISHMENT OF THE NORTH TEMPERATE LAKES DATA SYSTEM

a. Introduction

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

The choices of lakes and measurements were guided by a desire to identify and answer 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) 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.

b. Results

(1) Lake and Measurement Choice

Following considerable preliminary analysis and discussion of lake choice at our first External Review Committee meeting, we focused on a suite of lakes linked through a common groundwater and surface flow system as well as common climatic, edaphic, and biogeographic systems (Fig. 1). The suite includes oligotrophic, dystrophic, and mesotrophic lakes. 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). We collect a complete set of biological, chemical, and physical data on the primary lakes.

We also have secondary lakes on which less complete data are collected. The choice of secondary lakes and measurements on them 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 more influenced by year-to-year changes in weather. Our secondary lakes are: Clear, Escanaba, Firefly (Weber), Little Rock, Mary, Mendota, Mystery, Nebish, and Pallette. Lake Mendota is our only study lake located outside the Northern Highlands area. We have included it because of marked differences in its biota, chemical conditions and trophic status relative to our other lakes. Also, there are extensive and historical data available for Mendota.

In general, we chose the lakes, not only for their diversity, but also for their connection or relatedness through common groundwater, edaphic, climatic and biogeographic systems to facilitate landscape as well as long-term ecological research. Also by the choice of primary lakes, groundwater, based on 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 1981), becomes one central focus of our LTER on north temperate lakes.

We also spent considerable effort designing and implementing a balanced and integrated data collection program (Kratz et al. in press). Our sampling program (Table 2) allows comparisons of parameters among seasons, years, and lakes. We sample most major physical and chemical parameters. Likewise, information is collected on all trophic levels from primary producers to top consumers. On each lake we have established a central station (Fig. 2) where most related physical, chemical and biological parameters are measured at the same time of day.

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. Zooplankton and phytoplankton are sampled three times at bi- or triweekly intervals during these four periods, except during winter, when samples are taken every 5 weeks. Our sampling scheme facilitates comparisons of parameters among seasons, years, or lakes. The ability to make statistical comparisons is critical to detect long-term trends.

We have attempted to match the frequency of sampling as closely as practically possible with the appropriate time scale for the dynamics of each parameter. Between the intensive quarterly sampling periods, phytoplankton and zooplankton samples are usually collected biweekly although the sampling frequency is reduced to monthly when water temperatures are low. Temperature, dissolved oxygen, chlorophyll a, and nutrient profiles are measured in each lake every 2 or 3 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.

On occasion we have modified or developed measurement techniques. For examples, 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 (Appendix 3) (Clay 1983, Rudstam et al. manuscript); and we have evaluated the problems of measurement of thermal properties of multibasin lakes like Trout Lake (Robertson 1984).

(2) Inventory of 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. 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. Major portions of the water chemistry, phytoplankton, and zooplankton data have been computerized by various agencies. The historical data are described in more detail in Lehner (1980) and Lehner et al. (1980). In addition we gathered historic maps and documents relevant to the site. These are now available at the Trout Lake Station and the Laboratory of Limnology. Some of our uses of these data are described below (page 9).

(3) Data Management

Building on the computational facilities available through the Madison Area Computing Center (MACC), we developed a database system using microcomputers (Apple IIe). We have used the microcomputers for data entry, data reduction, data transmission, and statistical/graphical analysis. Storage and handling of full-record files are accomplished using the SIR data base and the Sperry-Univac 1180 at MACC. Generally data flow from Trout Lake Station and the geochemistry laboratory (Madison) through the data manager, the data base at MACC, and into "report" form (Fig. 3). Records of data at various stages are archived, and available to users in forms ranging from unverified, raw data to error checked, to finalized data files available from the SIR databases.

We developed extensive software during the first 2-3 years, with special attention paid to data reduction programs for pH, alkalinity, and chlorophyll and to a graphics program which allows early screening of erroneous data by the site manager and data collection crew. We developed a data entry program for the Apple II that features form design, matrix fields for input, and textfile output for transfer to the mainframe database.

We are presently re-evaluating our database and data analysis needs, and considering use of the UNIX based "ingres", and "S", a graphical and statistical analysis package. Our consideration of alternate data analysis systems arises in part from intersite activities from other LTER programs that use such software such as Jornada and Central Plains Experimental Reserve.

c. Proposed Research

We propose to continue the base sampling and data collection (Table 2) started in the first five years (Magnuson et al. 1984, Kratz et al. in press). Experience gained from the first five years coupled with principles derived from hierarchy theory (section F) will guide our efforts to improve and refine the sampling scheme. We will expand our regular data collection in two areas early in the next five years.

First, we will extend our analyses in time using sediment cores from each of the primary lakes. The cores will be available both to LTER and related projects. Initial analyses will be for fossil pigments, and a reconstruction of past primary production and perhaps algal community structure. Later, the same cores will be used for sediment mineralogy, pollen, charcoal, diatoms, and zooplankton.

Second, we shall upgrade our meterological record by developing the capability to continuously measure temperature, relative humidity, wind speed and direction, solar radiation (PAR and total), and precipitation from a raft on Trout Lake. This capability will help us analyze the importance of climate as an external control on lake processes.

2. LONG-TERM CHANGES AND THE USE OF HISTORIC DATA

a. Introduction

Our early efforts to examine long-term changes in lake ecosystems include comparisons of early Birge and Juday data with current LTER measurements, evaluation of bias in long-term weather data, and the examination of existing long-term data from Escanaba Lake, WI and Lake Windermere UK to gain familiarity with some of the problems and opportunities to be presented in the future with LTER data.

b. Results

(1) Comparing Recent Data with Historic Measurements

Birge and Juday data, collected from 1925 -1942, are being compared with recent data on water chemistry, climate and physical limnology, plankton, macrophytes, and fishes. It appears that, although lake parameters may have fluctuated or cycled in the last 50 years, they have not changed dramatically. LTER lakes have not become culturally acidified based on lake chemistry. The same taxa of plankton and macrophytes are present within lakes and, while a few new fish species are present, extinctions have been rare. Even though larger unidirectional changes may occur in the future (page 38) we appear to be working with a system that has been relatively unaffected by human activities at least since the logging and burning of the forests from 1900 to 1930. We present here three historical comparisons, on climate, water chemistry, and fishes.

Meterological Data from Rhinelander, WI. Recent examination of meterological data from a weather station 48 km from Trout Lake points out a common but worrisome problem in the interpretation of long-term patterns in air temperature data obtained from max-min thermometers. Average maximum and minimum readings are often used to estimate mean daily temperatures, which are, in turn, averaged to estimate mean annual temperatures. Baker (1975) demonstrated that the time at which a max-min thermometer is read, can bias annual mean temperature calculations by as much as 1.0°C. Robertson (Bowser in press) applied Baker's corrections to data from Rhinelander WI (Fig. 4). Uncorrected values show a step decrease in temperature when the time of observation was changed from 0700 to 1700 hrs in 1970. The step change disappears in the corrected series. Major interpretive errors on the effect of climate as a external driving variable can be made if we are ignorant of such calibration problems in existing long-term data.

Water Chemistry. Alkalinity, pH, and conductivity of surface waters of our oligotrophic and mesotrophic lakes increased slightly (Fig. 5) even though some of the lakes are classified as sensitive to acid loading (Eilers et al. 1983). The increases were greatest in mesotrophic Trout Lake, a drainage lake, that is low in our groundwater system. In contrast, oligotrophic Crystal Lake which is primarily a groundwater recharge lake and Big Muskellunge Lake, high in our groundwater system showed the least change. Groundwater-lake interactions play an important role in determining the ion composition of lake water (Chen et al. 1984). We hypothesize that these 50-year changes are more consistent with forest regrowth and increases in groundwater gradients, than they are with effects of anthropogenic increases in acidic deposition (Bowser et al. manuscript). Long-term experiments are planned (page 13) to test these ideas.

Fishes. Cisco (*Coregonus artedii*), a pelagic, zooplanktivorous fish, is abundant in the cold waters of the deeper LTER lakes. Recent data from Rudstam (1984) have been compared with estimates by Hile (1936) to evaluate changes in this species. Our acoustic estimate of cisco abundance in Trout Lake (Rudstam et al. MS) was 1.35 million fish in August 1981 or about 0.4 cisco per m^2 of lake surface. Comparisons of gillnet catches indicate that current conditions of abundance and growth in Trout Lake are not different than the parameters estimated by Hile. In contrast, cisco in Big Muskellunge and Sparkling Lakes are slightly less abundant now and, apparently owing to density dependent factors, are growing faster. This indicates that factors associated with individual lakes exert a major control over cisco populations. Additional evidence for this explanation derives from both Hile (1936) and Rudstam (1984) who found that year class success of cisco was asynchronous among lakes. In Sweden the related vendace (*Coregonus albula*) fluctuates in regular two year cycles indicating the presence of strong feedback control within a lake (Hamrin 1979). Apparently reproductive success of cisco in Northern Highland Lakes is not controlled primarily by an external climatic signal.

(2) Experience with Long-term Data

To gain experience with long-term limnological data we are analyzing existing records in Lake Escanaba, WI and Lake Windermere UK.

25 Years of Growth Data on Competing Piscivores. Fish populations of Escanaba Lake, one of our secondary lakes, have been monitored since about 1954 by the Wisconsin Department of Natural Resources. Two congeners, the northern pike (*Esox lucius*) and the muskellunge (*E. masquinongy*), occur in the lake and have a history of population antagonism (Inskip and Magnuson 1983). Year to year changes in both yearling growth and condition of adults were positively correlated between pike and muskellunge (Inskip and Magnuson in press). Correlation coefficients were +0.65 and +0.77. The two species have similar diets and we hypothesize that the temporal correspondence in growth and condition resulted from exploitation competition for food. Statistical associations with 25 years of data on the abundance of pike and muskellunge and their primary prey, the yellow perch (*Perca flavescens*), support our contention. Fluctuations in numbers of the abundant pike induced density dependent growth responses in both congeneric top predators.

40 Years of Growth Data on Northern Pike. The Windermere Laboratory of the Freshwater Biological Association UK have amassed extensive long-term data on fish, plankton; chemistry and physical limnology. In 1984 Magnuson spent part of his research leave at Windermere. Fish data were made available by Dir.

Robin Clark and Drs. Kippling and LeCren. The data are being analyzed but are presented in their raw form here to demonstrate 1) the occurrence of cyclic patterns of different period, and 2) the complexity of related time series data.

Growth of yearling pike (Fig. 6D) should increase with water temperature (Fig. 6A, B, & C); greater abundance of their principal prey, young-of-the-year perch (Fig. 6F); and decrease with the abundance of their principal competitor for young perch, the young-of-the-year pike (Fig. 6E). A multiple linear regression model for yearling pike growth as a function of summer degree days, winter degree days, young-of-the-year perch abundance and young-of-the-year pike abundance shows a significant relationship but explains only 32 percent of the variation in growth ($F_{4,31}$ =3.6, $p < 0.025$). A time series model may be more powerful because it includes information on the temporal regularity in the data.

The growth of yearling pike appears to demonstrate a 4 year periodicity with a growth minimum every 4th year (Fig. 6D). Summer temperature data appear to have a 2 year periodicity (Fig. 6A) as indicated by a recurring saw tooth pattern. Other frequencies and random walks may also be in these results. A long time series and time series statistical techniques are required to test whether the 2 and 4 year periodicities actually occur regularly. For example an attempt to detect a 4 year period in any 5-year segment (Fig. 6D) is impossible and in any 10-year period is less than convincing. Without time series techniques even the apparent regularity of a 38 year series of pike growth has no statistical justification.

c. Proposed Research

The growing time series of LTER data will be used to ask and answer the questions developed in our major objectives (sections B(2)c - E). Ultimately, when sufficiently long (20 years) periods are available, we also will examine the long-term trends and periodic behavior of key limnological parameters using time series techniques.

We will continue to compare our LTER data with Birge and Juday data. In particular a graduate student of Dr. Tom Brock is comparing the historical phytoplankton data with recent results. We also will compare zooplankton data and additional water chemistry data.

We propose to develop the time series model for the growth of pike in Lake Windermere, UK and test it on Lake Escanaba, WI The project is conducted jointly with Drs. LeCren, Kipling, and Tunnicliffe-Wilson of the UK and Drs. Magnuson and Mr. Serns (Wisconsin Department of Natural Resources) of the U.S.A.

We propose to apply time series techniques to the analysis of available long-term series data at our site. These will include weather data from 1903 to present near Trout Lake and also the longest limnological record in Wisconsin - ice cover dates for Lake Mendota from 1856 to present or ca 130 years. These ice cover data will be analyzed in respect to local weather at Madison, WI and long-term patterns in world climate.

C. UNDERSTANDING THE DYNAMICS OF INTERNAL AND EXTERNAL PROCESSES AFFECTING LAKE ECOSYSTEMS

1. INTRODUCTION

External factors, through variation in climatic and hydrologic inputs initiate temporal changes in the structure and processes of lake ecosystems. Internal processes also produce temporal patterns in lake ecosystems. We are interested in how the time course of these external and internal process interact to generate the long-term dynamics observed in lake ecosystems. An understanding of long-term patterns in lake ecosystems must be based on determinations of important linkages among lake processes and on the long-term dynamics of such linkages.

Climate exhibits several patterns of long term variability. Year to year variation is substantial (Madden 1977) and provides a major gradient against which to measure responses of lakes. Climate also exhibits distinct long-term cyclic behavior and trends with a general warming of the northern hemisphere in the period immediately preceding the 1930's and a cooling since that time (Jones et al. 1982).

Groundwater is a major component of the hydrologic and chemical budgets of the primary LTER lakes. Relative to precipitation and surface runoff, ground waters have low frequency responses and, therefore, can potentially cause long lags in the response of lakes to changes in chemistry of precipitation or forest cover.

Internal processes are likely to operate with relatively short time lags ranging from days to a few years. Primary production in a lake might respond 1) within days or weeks to changes in external nutrient loading, 2) within a year to internal P loading determined by a previous summer's hypolimnetic oxygen deficit or by the extent of turnover the previous autumn, or 3) within a few years to increased zooplanktivory resulting from a strong year class of perch. All of these short time lag events, however, are driven by the forcing factors of climate and hydrology which have components of variation that operate over time scales ranging from decades to centuries. Fish year class strengths may be linked to climatic cycles with twenty year periods. Nutrient loading via groundwater may result from a clear-cut that occurred 60 years before. Predictive models of the dynamics of lake productivity, for example, must include the ways in which a suite of internal, short time-lag factors are linked to the external, long period factors.

2. EXTERNAL PROCESSES

Climate, fluxes of water, and transport of materials and organisms from surrounding areas provide important external controls on lake ecosystems.

a. **Climate**

(1) **Introduction**

In examining interactions between lakes and climate, we examine the response of physical lake parameters to year to year differences in climate and the links between physical characteristics and chemical or biological features of lake ecosystems.

Numerous physical characteristics of lakes are controlled to a great extent by climate, including dates of freezing and opening, temperature of the epilimnion, surface temperature, depth and sharpness of the thermocline, maximum temperature of the hypolimnion, and the annual heat budget. Most studies relating thermal responses of lakes to climate have dealt with many lakes from different climatic regions (Birge 1915, Hutchinson 1957, McFadden 1965, Ragotzkie 1978, Shuter et al. 1983). This approach underplays the interaction of climate with lake morphology, altitude, or local setting in determining physical characteristics. An alternative approach is to examine a lake in the same region for a long time (Stauffer and Armstrong 1984, Strub et al. 1985), but such data sets usually are neither long enough nor include enough lakes.

The LTER lakes provide a gradient against which to measure interactions of climate and lake morphology in determining the thermal features of lakes. Our primary LTER lakes are subjected to nearly identical climatic conditions, but the lakes differ in morphology and each responds to climate differently. Small shallow lakes like Crystal Bog should respond more rapidly to climatic fluctuations than would the chemolimnion of meromictic Lake Mary which may respond in decades or even longer.

(2) **Results**

Research to date has focused on 1) gathering physical limnological data on the LTER lakes (published and unpublished), 2) compiling and correcting data on climate from 9 sites (Appendix 4) within 50 km of the primary LTER lakes, and 3) conducting preliminary statistical analyses of the relationships between climatic variables and lake parameters. For Trout Lake, simple regression analyses indicated that mean winter temperature was a fairly precise predictor of the duration of ice cover (r^2 = .60). In contrast, although a significant relationship exists between mean spring air temperature and the mean midsummer temperature of hypolimnetic waters ($p < .05$), the relationship is imprecise (r^2=.17).

(3) Proposed Research

Our research on climate centers on three questions.

1) <u>Do climatic factors induce predictable year to year variation in thermal conditions within lakes?</u>

Our goal is to explore the relations between climate and physical lake parameters using sophisticated statistical approaches including multiple regression and ordination. We intend to develop predictive models for parameters such as annual heat budget, hypolimnetic temperature, and length of ice cover for example., based on combinations of climatological variables such as average monthly values of temperature, wind speed and direction, precipitation and solar radiation. Intermittent records of year to year change in physical limnology then will be extended to develop a complete time series from 1903 to the present.

2) <u>How do differences in lake morphology affect the nature and the time scale of a lake's physical responses to climatic variation?</u>

We predict that the varied morphologies of the LTER lakes will lead to varied physical responses within lakes subject to essentially the same climate. Deviations in the thermal responses of particular lakes from the predictions of general models employing climatic parameters as independent variables will depend on the effects of morphological and landscape features in mediating thermal behavior. By expanding our analyses to include parameters related to landscape and morphology and by shifting the time periods from which predictions are made, we will determine the specific roles of these parameters and their effects on the time-lags in lake ecosystems.

3) How do lake features related to climate affect chemical and biological patterns and processes occurring within lakes?

Although the effects of climate on certain lake parameters (e.g. primary production) may be relatively straightforward, many additional variables should respond to climate in subtle ways. Fish year class strengths may be effected by temperature conditions during spring in shallow waters. Hypolimnetic oxygen depletion may be controlled by air temperature in the week immediately prior to stratification. The amount of nutrients distributed within a lake at turnover is likely to be controlled by wind speed and direction during a one week period. By considering common features in the LTER lakes within a year and contrasting those features with among year differences, we will gain insight into the controlling effects of climatological features.

b. Groundwater

(1) Introduction

The LTER lakes can be considered as nodes of open water within a continuous sheet of groundwater flowing through the sandy till of the Northern Highlands. Groundwater discharges into the lakes and similarly the lakes make a major contribution to the groundwater. Chemical reactions occur as water flows through soil and rock and have a major effect on groundwater and subsequently lake chemistry (Winter 1978, Likens et al. 1977, Crowe and Schwartz 1981 a,b, Frape et al. 1984, Hurley et al. 1985). Conversely, major inputs of relatively dilute lake water into the groundwater also may have important effects on the groundwater. Thus, substantial hydrological and chemical interactions occur between groundwater and lake. These processes have been a major focus of our research.

(2) Results

Groundwater effects on lakes. Okwueze (1983) used shallow seismic and electrical logging techniques to determine regional groundwater flow patterns in the area surrounding our primary LTER lakes (Fig. 1). He also measured depth to bedrock to allow better estimates of regional flow patterns. His maps provide basic information for groundwater flow models.

Drawing on information from a network of monitoring wells Kenoyer (in preparation) established that Crystal Lake's hydrologic inputs are dominated almost exclusively by precipitation with outflow occurring through groundwater. Groundwater input to the lake was limited to a small discharge following early spring snowmelt. Although the quantity of water that entered the lake through groundwater was minor, its impact on nutrient conditions in the lake was significant (Hurley et al. 1985). The spring groundwater discharge exhibited high solute concentrations compared with the lake water, particularly for dissolved reactive silica, and exerted a major influence on both diatom and overall production in Crystal Lake (Table 3).

Krabbenhoft (1984) examined spatial heterogeneity in groundwater flow into the east side of Trout Lake using wells and seepage meters. He determined that gravel lenses substantially increased groundwater inflow at some points on the lake shore (Fig. 7). Groundwater entering the lake exhibited high concentrations of iron and manganese, and areas of major inflow were associated with large deposits of ferromangese nodules.

Groundwater inflow also appears to influence physical and biological lake features. Discharge of warm groundwater along the east side of Trout Lake alters its thermal structure under ice cover (Robertson 1984). Extensive beds of macrophytes in Sparkling Lake appear to be associated with areas of high inflows of groundwater (Lodge et al. in preparation).

The groundwater system also provides substantial temporal buffering of the effects on lakes of annual changes in rainfall and of long term changes in precipitation chemistry. Because surface runoff to the LTER lakes is insignificant and the velocity of groundwater flow is low (approximately 50 years per km), the effects on lake chemistry may lag substantially behind a shift in atmospheric chemistry (e.g. acid precipitation), even when chemical buffering in the groundwater is not considered (Fig. 8). Because the relative contribution of groundwater to the LTER lakes is highly varied, time lags also would be different among lakes.

Lake effects on Groundwater. Data from a network of wells on the isthmus separating Crystal Lake from Big Muskellunge Lake reveals substantial shifts in chemistry as dilute water enters the groundwater from Crystal Lake and flows towards Big Muskellunge (Fig. 9) (Kenoyer in preparation, Kenoyer et al. in preparation). Significant increase in dissolved solutes occur within 250 m of Crystal Lake. Mineral equilibrium/speciation modeling of groundwater chemistry indicates the major importance of silicate minerals in this system. Alkalinity distribution within this flow system indicate that carbon sources for silicate dissolution derive partly from atmospheric CO_2 and partly from particulate organic carbon within the tills.

Dilute bog-lake water moves downgradient into the peatland surrounding Crystal Bog (Lake 27-2) to produce spatial gradients in the chemistry of interstitial waters (Fig. 10). The area, extent, and chemistry of the plume change seasonally, apparently as a function of water-table level. Dramatic differences in interstitial water chemistry occur over relatively short horizontal distances in the peatland. These differences may have subsequent effects on bog organisms. For example, black spruce (Picea mariana) grows faster on the upstream side of the lake where interstitial water exhibits higher solute concentrations.

(3) Proposed Research

Examination of groundwater-lake interactions will focus on 1) developing mass budgets for critical solutes in LTER lakes, 2) determining linkages between groundwater inputs and within-lake processes, and 3) modeling the time course of groundwater flow and chemical reactions within the till surrounding the LTER lakes. We also will examine direct responses of groundwater to experimental manipulations of the forest cover. The following questions summarize our proposed work.

1) How do temporal variations in the chemistry of groundwater entering a lake influence overall lake chemistry?

We will initiate detailed physical and hydrogeochemical analyses of Sparkling Lake, which is characterized as a groundwater flow through system receiving substantial inputs of groundwater. It contrasts sharply with Crystal lake where hydrologic inputs are dominated by precipitation. Results will be integrated using mass-transport flow and geochemical models to investigate time lags and year to year variability in nutrient inputs. Variations in input will be linked to the status of nutrient and trophic conditions in the lake.

Sparkling Lake is located within 3 km of Little Rock Lake for which detailed groundwater studies are currently being conducted as part of an experimental lake acidification study (section F, Appendix 5). This proximity provides a tie between studies of groundwater and chemical evolution in the chain of lakes from Little Rock (precipitation dominated) to Sparkling Lake to Trout Lake, a discharge lake where groundwater inputs dominate.

2) Does water discharged from lakes into the groundwater system influence terrestrial ecosystems?

We will continue to examine the chemical evolution in groundwater in the isthmus separating Crystal Lake from Big Muskellunge Lake. Geochemical models, emphasizing the role of dissolved CO_2, will be refined using quarterly data on hydrology and chemistry. Eventually this model will be expanded for use with other lakes in the area.

Studies will continue on the plume of dilute water extending into the groundwater system surrounding Crystal Bog. We will model the physical and chemical processes leading to spatial and temporal patterns in the peatland and investigate the effect of these patterns on the dynamics of peatland vegetation.

3) To what extent does groundwater flow buffer lakes against short term changes in precipitation chemistry?

The models that we have developed to examine time lags in lake responses to groundwater will be expanded to include considerations of solution chemistry within the groundwater system. Field studies on Crystal and Sparkling Lakes will be used for validation.

4) What effects do terrestrial disturbances (e.g. clear-cutting) have in regulating solute inputs to lakes via groundwater?

Because of large time lags after water enters the groundwater and when it reaches a lake, some groundwater now entering the LTER lakes may have been affected by forest use early in the century. Much of the Northern Highlands State Forest was clear-cut and burned in the 1910's and 1920's (Curtis 1959, Gage and Vanderschaegen 1983).

Previous studies have documented effects of clear-cutting on groundwater level (Urie 1977, Verry 1980), soil organic matter (Covington 1981), carbon dioxide efflux rates (Edwards and Ross-Todd 1983), nitrogen cycling (Krause 1982), phosphorus cycling (Wood et al. 1984) and net primary production (Likens et al. 1977, Borman and Likens 1979). These studies, however, have not considered the effects of clear-cutting on the soil P-CO_2 and its potentially important effects on the weathering rate in groundwater solutions. Because groundwaters are not in equilibrium with silicate phases in Northern Highlands tills, changes in groundwater chemistry could be caused by change in the transport rate of groundwater related to groundwater gradients, or by change in the reaction rate of groundwaters determined by variations in the partial pressure of CO_2 (Helgeson et al. 1969, Drever 1982).

We propose to study the changes in groundwater chemistry and flow that result from clear-cutting. We plan to instrument two small areas, one in a predominantly deciduous forest (poplar, birch, maple) and another in a predominantly coniferous forest (spruce, pine). A portion of each area will be clear-cut and we will compare groundwater levels and gradients, and soil and groundwater chemistry for several years between clear-cut and adjacent reference areas. Our results will be interpreted in respect to the long-term changes expected in lake chemistry following clear-cutting.

3. INTERNAL PROCESSES

a. Introduction

In addition to the external factors described above, many processes operate within a lake to effect the dynamics of features such as production and nutrient cycling. For example, regeneration of nutrients from sediments or from processes occurring within the water column will interact with external loading to control primary production. Processes may range from inorganic chemical reactions (e.g. phosphorus precipitation by iron) to biologically mediated uptake (e.g. P use by phytoplankton) and release activities (e.g. release of P from phytoplankton as they are consumed by zooplankton).

We are interested in the role that internal linkages play in determining the magnitude and temporal pattern of changes in lake ecosystems. Likewise, we consider the relative importance of biologically mediated processes relative to internal and external physical and chemical forces in their effects at population, community and ecosystem levels in lakes. Progress in these areas also requires an understanding of internal processes themselves.

Although numerous, interrelated physical, chemical, and biological factors control primary production in lakes, the supply of essential nutrients in available forms to the photic zone and removal processes such as herbivory are among the most important (Reynolds 1984). Any of several essential nutrients (C, N, P, and Si) may regulate primary production, but phytoplankton populations are not viewed as being limited by a single nutrient. Dominance among phytoplankton species depends on concentrations and ratios of essential nutrients (Reynolds 1984). Resource-ratio gradients may also influence the composition and dominance of phytoplankton assemblages (Reynolds 1984, Kilham and Kilham 1980, Tilman 1977). Several investigations (e.g. Schindler 1978, Edmondson and Lehman 1981, Stauffer 1985) have linked primary production or trophic status to phosphorus loading or concentration. However, in some instances nitrogen (Smith 1982), silica (Hurley et al. 1985) or perhaps carbon (Reynolds 1984) may be limiting.

While the gross level of limnetic productivity apparently is set by nutrient loading and internal cycling (Schindler 1978), at any given nutrient concentration (phosphorus for example), chlorophyll and productivity may vary greatly as governed by size size-structured trophic interactions (Carpenter and Kitchell 1984, Pace 1984). Stocking of piscivorous fishes and elimination of planktivorous fishes in a north temperate lake led to increases in the mean size of zooplankters and a doubling of the grazing pressure on phytoplankton (Shapiro and Wright 1984). Phytoplankton abundance and chlorophyll concentrations dropped while Secchi depth increased. These changes could not be explained by changes in nutrient concentrations (Wright and Shapiro 1984). Similar results come from other manipulative lake studies (Benndorf et al. 1984), with impacts of increased water clarity (with high piscivore densities) extending to the benthic community (Spencer and King 1984).

Understanding the way information flows from one trophic level to the next has been a major goal in ecology (Margalef 1968, Allen and Starr 1982). Major uncertainty exists over the relative importance of biotic versus abiotic forces in determining both ecosystem processes (O'Neill 1976) and the distribution and abundance of species (Strong et al. 1984). For example, the size structure of a zooplankton community may be influenced by the physical environment, by aspects of available food resources (bottom up control), and by predators (top down control). There is mounting evidence that under certain conditions even the lowest trophic levels are influenced by top carnivores through a chain of cascading trophic interactions (Carpenter in press). Changes in nutrient loading also can dramatically alter phytoplankton community structure and primary productivity (Schindler 1978, Edmondson and Lehman 1981) and in some cases affect growth and abundance of fishes (Warren 1971, Carpenter et al. in press). However various signals will be dampened or possibly even enhanced by trophic interactions. Conditions promoting, dampening, or enhancing transfer of information upward or downward across trophic levels remain to be evaluated.

The relative importance of these factors will vary in space among LTER lakes and in time within each lake.

b. Results.

We have studied both nutrient cycling and its potential role in production and changes in the abundance of consumer populations to evaluate their influence over production.

(1) Silica Dynamics in Crystal and Sparkling Lakes.

Primary control over the nutrient status of lakes is usually exerted by recycling from bottom sediments and allochthonous inputs. Nutrient input from groundwater has usually been neglected as a direct measurement. Analyses of internal cycling of silica in Crystal Lake derived from sediment trap data, water chemistry, sediment composition, sedimentation rates were contrasted with direct determinations of groundwater. By contrasting internal cycling of silica with groundwater input (Table 3) it was possible to determine that groundwater is a crucial source of nutrients for Crystal Lake (Hurley et al. 1985).

Over three years Crystal Lake shows a dynamic but consistent pattern in silica concentrations (Fig. 11). Dissolved reactive silica (DRSi) is depleted in the spring. Reductions in DRSi are mirrored by increased in chlorophyll and particulate biogenic silica indicating a strong link between silica supply and diatom production. During fall and winter dissolved reactive silica concentrations show a persistent increase due to regeneration from sediments and a relatively small inflow of groundwater with high silica concentrations.

Using the same basic methods, we contrasted conditions between Crystal Lake with Sparkling and Trout Lakes. This comparison was of interest in part because silica limitation of diatoms may occur when the Si:P ratio is less than about 90 (Tilman 1977, Holm and Armstrong 1981). This condition is likely to occur in lakes with a predominant hydrologic input through precipitation (e.g. Crystal) but not where groundwater dominates (e.g. Sparkling).

Silica depletion is not evident in Sparkling and Trout Lakes (Fig. 11). Although chlorophyll and PBSi data show diatoms are important in these lakes, the available DRSi supply does not appear to limit diatom production. Apparently, groundwater inflow maintains a relatively high DRSi concentration, masking utilization by diatoms. The high and relatively invarient DRSi concentrations in Sparkling and Trout reflect the major influence of the groundwater-lake water linkage in these two lakes.

Despite the critical role of groundwater in these lakes, our studies also indicate the major influence of silica regeneration from sediments. Recycling from sediments accounts for the relatively high amounts of diatom related production in Crystal Lake, an amount that is substantially higher than can be accounted for by groundwater inputs (Hurley et al. 1985). Over one-half of the silica supply in Crystal Lake results from regeneration from sediments.

Internal loading from sediments may occur through either physical-chemical or biological processes. Aquatic macrophytes may transfer phosphorus from the sediments into the water column (Prentki et al. 1979, Carpenter 1980). Diagenesis of phosphorus, nitrogen and silica in sediment leads to high pore water concentrations and transfer to overlying lakes waters (Jones and Bowser 1978). Diffusion rates may be accelerated by physical mixing or bioturbation. Release of phosphorus is facilitated by anoxic conditions (Mayer et al. 1982) but may also be important for oxygenated sediments (Twinch and Peters 1984). Wind-induced eddy diffusion and thermocline migration enhance transport to the photic zone (Stauffer and Armstrong 1984).

Recycling behavior of silica is different in Sparkling Lake. This may be linked with upper trophic level interactions. Fecal pellets from calanoid copepods are abundant in sediment traps in Crystal Lake but are absent in Sparkling Lake (Hurley 1984). Diatom ingestion by zooplankton and subsequent transport to sediments may influence re-release rates. Alternatively, chemical conditions in Crystal Lake sediments may retard silica dissolution.

(2) Iron Transport from Groundwater to Lake Sediments.

Phosphate is readily absorbed by iron in sediments and thus, the cycles of these two elements in lakes are related significantly (Koenings and Hooper 1976). Phosphorus limitation in the LTER lakes is enhanced by iron-rich sediments (Williams et al. 1971) and by high Fe:P ratios in sediments and anoxic bottom and pore waters which facilitate both P retention in sediments and scavenging of P from lake waters by Fe (Mayer et al. 1982, Stauffer and Armstrong 1984, Stauffer 1985). Retention of P in the sediments by iron is more important in Sparkling and Trout Lakes when compared to Crystal Lake. This is related to patterns of groundwater discharge which transports substantially more dissolved iron into the sediments of Trout and Sparkling. Mass budget calculations indicated the importance of direct iron inputs to Trout Lake via groundwater (Krabbenhoft 1984). Still, scavenging by Fe is important even in Crystal lake in which Fe is apparently supplied to lake water from sediments despite a predominance of oxygenated water column conditions throughout the year (Hurley 1984).

(3) Shifts in Trophic Structure

Although we have not measured interactions between adjacent trophic levels directly, we have documented distinct shifts within trophic levels. Such shifts indicate that linkages among tophic levels would undergo substantial changes in magnitude and, possibly direction of influence.

Detailed analyses of zooplankton populations in Crystal Bog revealed major differences between summer and winter zooplankton communities (Fig. 12). Predominant taxa shift dramatically between seasons although biomass appears to be relatively constant between the two periods. These differences may relate to differences in food availability between summer and winter.

Lyons (1984) analyzed the role of large year classes of yellow perch (species) in buffering the effects of predation by walleye (Stizostedion vitreum) on other littoral zone fishes such as darters (Percidae) and minnows (Cyprinidae) in Sparkling Lake. There is a general association between warmer annual temperatures and year class strength in perch. When populations of young-of-the-year (YOY) perch are low predation by walleye has a major impact on

YOY perch, and adult darters and minnows. In contrast, in years when the number of YOY perch is high, walleye predation on darters is dramatically reduced. Summer mortality of adult minnows, however, did not decrease. Thus, year to year variation in the population of a particular fish species can have substantial direct and indirect effects on fish communities.

In contrast to the situation described above for perch, year class strengths for cisco are not associated with climate and substantial asynchrony of year classes occurs among LTER lakes (Rudstam 1984). Populations of cisco have decreased substantially in Big Muskellunge and Sparkling Lakes, while showing major increases in Trout Lake in the period from 1981 to 1984 (Table 4). Direct effects of cisco on lower trophic levels and indirect interactions with other fishes will shift substantially among lakes and among years.

c. **Proposed Research**

We will expand our considerations of the relative role of internal and external sources of nutrients. This work will be fostered by improvements in our determinations of primary production through the application of laboratory incubation techniques. Our emphasis will shift increasingly to comparison of processes among LTER lakes. Similarly, we will expand our considerations of trophic level interactions within the LTER lakes using a comparative approach combined with direct measurements of trophic interactions. At both levels comparisons will be drawn across both lakes and years.

1) How are year to year changes in lake production related to changes in loading and internal cycling of nutrients?

We will focus on the role of nutrients in controlling productivity by comparing parameters within lakes (temporally) and among lakes (spatially). Nutrient status will be determined from absolute values and ratios of in-lake concentrations as well as fluxes to the photic zone from internal and external sources (Tilman 1977, Schindler 1978). For example, the low concentrations and ratios of silica to other nutrients in Crystal Lake indicate that diatom production is silica limited (Hurley et al. 1985). Similar relationships will be evaluated for silica, nitrogen, and phosphorus among the lakes. With higher external silica loading (e.g. Sparkling Lake), phosphorus limitation and thus year to year changes in phosphorus are likely to control productivity.

Internal loading from bottom sediments will be evaluated using three approaches. The primary approach will involve mass balance determinations over periods of a few weeks on changes in in-lake nutrient content, nutrient external loading, and nutrient output (groundwater outflow, sedimentation) as described by Riley and Prepas (1984) and Hurley et al. (1985) . This will be supplemented by (1) calculations of transport by mixing of surface and bottom waters using heat as a tracer of mixing of surface and bottom waters (Riley and Prepas 1984, Stauffer and Armstrong 1984) and (2) calculation of transport by eddy diffusion from bottom to surface waters using the flux-gradient method (Jasby and Powell 1975, Stauffer and Armstrong 1984). The mass balance approach showed internal loading was a major source of silica to Crystal Lake (Hurley et al. 1985). Internal loading is also expected to be important for phosphorus (Stauffer and Armstrong 1984, Twinch and Peters 1984) but evaluation of the relative importance of internal versus external sources for P has not been completed.

The information on internal nutrient recycling combined with the information on external loading will be used to evaluate the relative importance of these two pathways. Evaluation of the lake features, among contrasting lakes, associated with a relatively high importance of internal loading will be useful in identifying lakes characteristics controlling differences in internal loading. For example, morphometry and anoxia are expected to be important in phosphorus internal loading (Mayer et al. 1982, Stauffer and Armstrong 1984).

Evaluation of sources to Crystal Lake (Hurley et al. 1985) showed internal recycling of silica from bottom sediments was of the same magnitude as external loading. With higher external silica loading (e.g. Sparkling), internal recycling may become relatively unimportant, and phosphorus internal loading may be a key factor in nutrient status.

2) Are year to year changes in lake productivity with similar nutrient inputs governed by trophic interactions?

To approach this question we will use food web and time series data on simultaneous population changes of fishes, zooplankton, phytoplankton, and nutrients. For example, concomitant with the decline in zooplanktivorous cisco that we have observed in Big Muskellunge Lake (Table 4), we predict that we will observe increases in 1) the mean size of zooplankton, 2) the rate of zooplankton herbivory, and 3) secchi depth and decreases in phytoplankton biomass and production. In Trout Lake, where cisco are increasing, we expect the opposite results. We will apply similar analyses to the seven primary LTER lakes. Major differences in morphology, trophic status, and fish community structure among these lakes should lead to significant differences in the relative importance of nutrient cycling versus trophic interactions and the complexity of the trophic effects. This should lead to differences in the temporal behavior of the lakes.

D. ANALYSIS OF THE TEMPORAL RESPONSES OF LAKE ECOSYSTEMS TO DISTURBANCE AND STRESS.

1. INTRODUCTION

Ecosystems exist in dynamic states as they respond to a series of quick-acting disturbances and long-term shifts in physical, chemical, and biological conditions. Analyses of the dynamic conditions in ecosystems and of responses to perturbations have become a major focus in ecological studies (Connell 1978, White 1979, Pickett and White in press).

Because disturbance is common to all ecosystems, recent work has attempted to provide a general format to explain the importance of various disturbances in different ecosystems (e.g. the LTER Disturbance Workshop). Such efforts have been hindered by inconsistencies in definitions of disturbance as applied to the dynamics of ecosystems. Inconsistencies derive in part from fundamental differences in the frequencies at which ecosystems change. For example, some may consider fire as a disturbance when it occurs every 100 years in a forest but not when it occurs every five years in a prairie; yet the process and response are similar. Definitions of disturbance that involve a deviation from a natural state of an ecosystem will necessarily lead to confusion because the natural state of a system is only defined relative to the period in which it has been studied.

Dynamic conditions within ecosystems also are driven by stresses, used here for events that operate over extended periods. Acid precipitation and species introductions are examples of longer term shifts in conditions. Actually, stress and disturbance could be treated as representing two ends of a spectrum in which the time over which impact occurs is a variable but in which a shift in ecosystem conditions is common.

Our approach will reveal the varied nature of responses of lake ecosystems to disturbance and stress and the lake features that influence such responses. The perspective to be gained from lakes is particularly valuable because some of the dynamics in lake ecosystems occur with frequencies short enough to allow measurements of numerous responses to perturbations. Thus we can examine the variability that occurs in responses to disturbance-like events rather than simply tracking one or a few events.

2. RESULTS

Our analyses of disturbance and stress have focused on turnover events, species invasions, and acid deposition.

a. Disturbance

Frost and White (manuscript) have suggested a definition of disturbance based on the disruption of conditions within an ecosystem. Disturbance is an event that 1) operates quickly relative to the life span of the organisms under consideration to 2) open ecological space, either directly in the case of a landslide or indirectly in the shifting of resource availability. Biotic activities (e.g. growth and competition) operate to fill space after disturbance. Using this definition we can consider different events (e.g. fire, landslides, volcanic eruptions, and treefalls) as the same basic phenomena and thus consider the frequency and spatial scale of disturbances among ecosystems. We also are interested in the variation in responses of ecosystems to repeated disturbance. From Frost and White's definition, most of our north temperate lakes could be considered as disturbed twice a year by turnover (Margalef 1968, Frost and Kratz manuscript).

Using a method described below (section E), we have analyzed the variability exhibited by zooplankton populations from several lakes in response to turnover as a disturbance over a series of years. The peak abundances reached by zooplankton populations are generally much more variable than the time at which a peak occurs. Similarly, copepods are fairly consistent in their spatial distribution relative to turnover but rotifers are much more variable.

In a similar analysis, the characteristics of a lake influenced the predictability of phytoplankton responses to turnover. Peak biomass (measured as chlorophyll-a) following spring overturn was more variable in lakes with lower conductivities (Crystal and Big Muskellunge; cc.v. = 60% and 50%) than in lakes with higher conductivities (Allequash, Sparkling, and Trout; cc.v. = 26%, 15%, and 33% respectively) (Fig. 13). (The differences in lake conductivities may reveal differences in groundwater input to the lakes, but we presently lack data to demonstrate this conclusively). Thus, the response of a system to repeated occurrences of a disturbance can be strongly influenced by factors external to the system.

We also study temporary ponds from a disturbance perspective where periodic flooding and drying have major effects on aquatic life. In inter-site activity at the Jornada LTER site we have assisted in a study on a playa lake which fills with water less than every ten years. In addition we have submitted a proposal to NSF-Ecology to support research on forest ponds at our LTER site in which flooded conditions vary in length from less than two weeks to greater than one year.

b. Species Invasions.

Lakes are island-like ecosystems, isolated to different extents from adjacent lakes (Barbour and Brown 1974, Magnuson 1976). Colonization of a new species becomes a key process, along with extinction, in altering biotic assemblages and trophic processes over time. Six of our seven primary lakes are not physically connected by streams, and migrations of fish and aquatic species of crayfish are slowed to the point of being rare. Two recent colonists, exotic to the region, have been establishing themselves since our work began - the rainbow smelt (Osmerus mordax) in Sparkling Lake and the rusty crayfish (Orconectes rusticus).

The rusty crayfish has expanded its range into northern Wisconsin lakes during the past 25 years. Transport by humans appears to have been a major influence in this expansion. It has had severe effects on aquatic macrophytes and fishes in many lakes. We have been monitoring the spread of the rusty crayfish within Trout lake over the last 12 years. The abundance of distribution (Fig. 14) of the native fantail crayfish (O. virilis) and two exotics, the blue crayfish (O. propinquus) and the rusty crayfish have changed from 1973 and 1983 in Trout Lake (Lodge et al. manuscript). Based on previous research (Magnuson et al. 1975, Lorman and Magnuson 1978, Stein 1977, Capelli 1982) we hypothesized that the blue crayfish which entered the lake about 30 years ago, would displace or cause the extinction of the native fantail crayfish. Eventually, we expected that the rusty crayfish would displace both the blue and fantail crayfishes and that the rusty crayfish would transform the littoral zone by the elimination of aquatic macrophytes and the reduction of benthic insects and fish reproductive success. To test these ideas, permanent stations, established around the lake from the site where the rusty crayfish was first observed in 1979, are sampled annually for crayfish, fish, benthic insects and macrophytes.

By 1973 the blue crayfish was already more abundant than the native fantail (Fig. 14). However, by 1983 the blue crayfish had declined while, at the same time, the rusty crayfish had established only a small population. We conclude: 1) the interactions between the blue and fantail crayfish do not result in a unidirectional decline in the fantail crayfish as we had hypothesized, and 2) population growth and dispersal within Trout Lake by the rusty crayfish is relatively slow.

An invasion by rainbow smelt of Sparkling Lake provides an open water parallel to the crayfish introductions in Trout Lake. Here exotic smelt are replacing native cisco (Table 4). We predicted that replacement would occur after our first observations of smelt based on previous studies (Christie 1974, Svardson 1976).

Species replacement by smelt is occurring more rapidly than we observed for crayfishes despite the similar longevities (approx. 5 years) for both invading species. This is not unexpected because the pelagic habitat is more homogeneous than the littoral zone where crayfish occur. Also fecundity of smelt is greater than in crayfish.

c. Acid Deposition

Acid deposition is an environmental stress of international importance (Flamm and Bangay 1981, National Academy of Sciences 1981, Beament et al. 1984, Altshuller and Linthurst 1984). Our North Temperate Lakes LTER site receives acid loading from the atmosphere, and many lakes in our region are potentially sensitive to acidification. Our research efforts have focused 1) on a detailed comparison of lake conditions at present with measurements recorded fifty years ago by Birge and Juday (Bowser et al. manuscript), 2) an analysis of the role of groundwater buffering in mitigating acidification and 3) a whole lake acidification on Little Rock Lake. Points 1 (page 9) and 2 (page 18) have been discussed above.

The Little Rock Lake Project was initiated in 1983 with funding by US-EPA. The program is projected for at least five years and involves investigators from five institutions (Appendix 5). Its primary purpose is to elucidate the mechanisms by which increasing acidity affects population, community and ecosystem level conditions in lakes. Little Rock Lake is a secondary LTER lake that lies within the same groundwater system as our primary lakes. Sampling on Little Rock has been designed to parallel LTER and there is close coordination between the two programs. The two basins of Little Rock lake were separated with a nylon curtain in fall 1984 and acidification begins at ice-out in spring 1985. Baseline data indicate that the two lake basins are similar for most physical, chemical, and biological parameters.

3. PROPOSED RESEARCH

In respect to disturbance and stress we will study not only turnover, but also watershed disruption (e.g. by fire or clear-cutting) and low dissolved oxygen as disturbance; and species invasions and acid precipitation as environmental stress.

1) How do the plankton respond to year-to-year variations in turnover as a disturbance?

In further studies of turnover we will expand our above analyses to include annual variation in physical and chemical parameters. We will also examine links between specific environmental parameters and biotic responses to turnover.

2) What role do terrestrial disturbances play in regulating nutrient input and production in lake ecosystems?

Investigations of watershed disruption will involve the direct experimental studies on the effects of clear-cutting on groundwater described previously (C) and paleolimnological investigations of fossil pigments to assess the response of primary production to forest fires. Several previous studies have revealed the utility of pigment analyses of lake cores in documenting past production levels (Sanger and Gorham 1972, Adams et al. 1978, Guilizzoni et al. 1981, Guilizzoni et al. 1982). Combining fossil pigment analyses with determinations of charcoal, pollen and diatoms will allow reconstructions of lake conditions before and after fire. In a related project, Armstrong has submitted a proposal to support a more detailed study of carotenoid pigments in lake cores. Armstrong's independent project will be conducted in close collaboration with our LTER work providing mutually beneficial interactions.

3) Is food web structure related to the magnitude and frequency of disturbance in lake ecosystems?

We will build on studies on winterkill lake ecology by Magnuson and his co-workers (Tonn and Magnuson 1982, Magnuson et al. 1983, Rahel 1984) by examining the relationship between food web structure and winter anoxia (Briand 1983, Briand and Cohen 1984). Food webs will be compared among lakes that vary in the degree and frequency of anoxia. We will test the basic prediction that predator:prey ratios and connectedness of food webs will be more predictable in lakes as the impact of anoxic conditions increases.

4) How are lake ecosystems response to stress related to the physical complexity of the environment?

We will continue following populations of native and invading species in Trout and Sparkling Lakes. This research will be particularly useful in documenting community and ecosystem level effects of invasions in addition to population shifts. Important insight into long-term processes will be gained from our comparisons of the difference in the time lags by which pelagic (homogeneous, simple) and littoral (heterogeneous, complex) environments are transformed by similar invasions of exotic species.

5) How does a complex lake-groundwater system respond to changes in acidic deposition?

Our research on acid rain will focus on the role of groundwater in buffering the effects of acid deposition falling in our study area (section C) and on our cooperative research on the Little Rock Lake experimental acidification (Appendix 5).

E. EVALUATION OF THE INTERACTION BETWEEN SPATIAL AND TEMPORAL VARIABILITY OF LAKE ECOSYSTEMS

1. INTRODUCTION

Traditionally, lake studies have emphasized heterogeneity within lakes and within years. A major strength of our LTER approach involves the expansion of these scales in space and time and, in particular, an analysis of the interactions at these broader scales.

A number of limnological studies have considered long time series for individual lakes (e.g. Lake Washington - Edmondson and Litt 1982; Lake Tahoe - Goldman 1981; Lake Windermere - Lund 1965). Similarly, a few synoptic surveys have considered a large number of lakes drawing information from only one or a few samples (Sprules 1975, Capelli and Magnuson 1983). Our study differs from these in that it examines seven lakes over the long term. Thus we can consider multiple scales of spatial and temporal variabilities and interactions between them.

Spatial and temporal variability in the occurrence of organisms can be used to assess the relative importance of climatic, edaphic, biotic, and stochastic forces in structuring communities. In examining sets of lakes within the same general region, it is possible to characterize limnological parameters as being associated with either lakes or years. For example, certain features, such as the presence of a species or the mean concentration of a nutrient, may be very specific to a particular lake. Year to year differences in such parameters would be relatively small compared to differences among lakes. Other lake features, such as zooplankton population levels and the day of maximum heat content might be specific to a particular year and relatively independent of lake. Lake specific parameters would be controlled by processes within lakes. Year specific features would be driven by external factors operating over an entire region.

We also expect that specific features of our lakes will exert a controlling influence over temporal variability. For example, annual variability in chemical, and subsequently, biological components of a lake should be related to its landscape position. In our LTER lakes, position within the groundwater flow system, and consequently the relative importance of groundwater inputs, may exert a strong influence on annual variability in nutrient availability and primary production. Similarly, the fish community structure of a lake is related to the landscape position of the lake and may also influence variability.

Finally, 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 hence act as a buffer against disturbance. We expect that increasing spatial heterogeneity will be associated with decreased temporal variability in populations and communities within lakes.

An understanding of the effects of both spatial and temporal heterogeneity is fundamental to an evaluation of the long-term processes affecting an ecosystem. Models predicting the response of biological parameters to the physical environment must account for the natural variability in biotic response. At the same time patterns of variability within systems can be contrasted with variability in external factors to evaluate the relative importance of internal versus external driving variables.

2. RESULTS

Our efforts to date have contrasted interlake and interyear variability of lake ecosystems.

Inter-lake versus inter-year variability. We have developed an analytical technique that assesses whether a particular limnological parameter is more strongly associated with lake or year. Using a matrix of parameter values in a set of lakes over a number of years we employ analyses of variance with variance partitioned in two ways. In one model, parameter values for each year are considered as replicates of conditions within lakes and a mean square is generated for differences among lakes. In the alternative model the same data are partitioned such that samples from each of the lakes are considered as replicates of conditions occurring within a year and a mean square is generated among years. The ratio of these two mean squares (among years/among lakes) is evaluated to determine the relative strength of a parameters association with lake or year. Although such a ratio can be evaluated with a standard F statistic, we have hesitated to base our evaluation on this test because we are uncertain as to how closely our data fulfill the assumptions for ANOVA. Instead we have contrasted the ratios themselves among our data to evaluate trends of association. Also, we have generated null matricies by assorting our parameters at random within the original lake-year matrix. We tested our values against those obtained in a thousand random simulations.

Analyses of Birge-Juday zooplankton data. We first applied this analytical approach to an extensive set of unpublished data on zooplankton that had been collected by Birge, Juday and their co-workers. Data were available for five lakes that were sampled concomitantly for a period of from 5 to 12 years.

Our analysis of zooplankton data collected by Birge and Juday in the 1930's revealed a correlation between life histories of zooplankton taxa and relative magnitudes of among year and among lake variation (Fig. 15). In general, taxa with lower reproductive potential (copepods and some cladocerans) exhibited more among lake than among year variation in abundance suggesting that internal lake conditions provide controls. In contrast, taxa with relatively high reproductive potentials (rotifers) showed approximately equal among year and among lake variability. This suggests that rotifers are responsive to annual variability caused by annual climatic variability. As lake conditions change, copepod and cladoceran taxa are likely to be influenced more than rotifers. We tested this hypothesis with zooplankton data from Lake Washington before and after sewage diversion (Edmondson and Litt 1982). After sewage diversion nutrient loading decreased dramatically altering edaphic and biotic conditions in the lake. Those zooplankton taxa that showed large among lake variability in the northern Wisconsin lakes (copepods and cladocerans) also changed abundance significantly after sewage diversion in Lake Washington. Consistent with the hypothesis, the rotifer taxa showed no significant change in abundance following sewage diversion.

Recent Fish Assemblages. We are applying other approaches to analyzing interyear and interlake variability using similarity indices with littoral zone fish assemblages in LTER lakes. In both abundance of individuals and their biomass, among lake similarities were equivalent to among year similarities in a single lake (Guo-Zhang and Magnuson manuscript) (Fig. 16). Thus, the assemblage in one LTER lake was as similar to that in another LTER lake as it was to itself in successive years. This large temporal variability in the littoral fish assemblages, results largely from variations in the abundance of young-of-the-year fishes and suggests that strong annual signals from the top trophic levels may be sent down through the food web.

3. PROPOSED RESEARCH

1) How are patterns of spatial and temporal variation in parameters related to the relative importance of climatic, edaphic, and biotic factors?

In extending our research on system variability we plan to consider physical and chemical parameters to complement the analyses of biotic features described above. This approach will be extended beyond lakes to other LTER sites (section F).

2) Do lakes whose productivity is limited by nutrients supplied largely by groundwater exhibit larger interyear variability in production than lakes whose limiting nutrients are supplied by other sources? and

3) Do lakes with simple fish communities (few taxa) show higher variability in fishes and lower trophic levels than lakes with complex fish communities (many taxa)?

Landscape position (i.e. degree of groundwater influence) and fish community structure are two parameters that exert important, and potentially interacting, influences over variability within our LTER lakes. We predict that lakes high in the groundwater flow system, additionally characterized by simple fish communities (e.g. Crystal Lake) will exhibit more annual variability in chemical and biotic features that lakes lower in the flow system with more complex community structure (e.g. Trout Lake). Observations of interyear variability in seven lakes will provide insight into the lake features that are important in determining the magnitude of interyear variability.

4) Is community heterogeneity a result of habitat complexity and social aggregation and does greater community heterogeneity produce less variability in levels of community productions?

Initially we propose to address this question with fish communities in the littoral zone. Several researchers have established a relation between habitat heterogeneity and the species richness of the littoral zone fish community (Rahel 1984, Tonn and Magnuson 1982, Eadie and Keast 1984) or investigated the factors involved in habitat partitioning (Werner et al. 1977). We propose to analyze the spatial distribution of the littoral zone fishes, to understand the factors which promote spatial heterogeneity in species composition (community heterogeneity) and the regulatory effects which such heterogeneity has on the fish community. We will focus on spatial scales within lakes and among lakes.

F. DEVELOPMENT AND TESTING CONCEPTS AND THEORIES RELATING TEMPORAL AND SPATIAL VARIABILITY OF LAKE ECOSYSTEMS AT SCALES RELEVANT TO LONG-TERM LANDSCAPE ECOLOGY

1. INTRODUCTION

Aquatic ecology and limnology have often been the source of major contributions to theory and concepts in general ecology. A few examples include the contributions of Lindeman (1942) in trophic ecology, of Hutchinson (1959, 1967) in niche concepts, and Hrbacek et al. (1961) and Brooks and Dodson (1965) in size selective predation.

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 system that are appropriate for lakes are distinctly different than those used in terrestrial systems. Likewise, physical features and the timing of events in aquatic system present major contrasts with forests, deserts, and grasslands. Despite these differences, general concepts in ecology must apply across terrestrial and aquatic systems. Explicit attempts by us and other investigators to include lake ecosystems along with terrestrial systems in overall LTER questions should help in the development of more general and robust ideas.

2. RESULTS

We participated in the intersite workshop on disturbance (page 32) and prepared two manuscripts on concepts of disturbance on lake ecosystems (Frost and Kratz manuscript), and on defining disturbance from a LTER research perspective (Frost and White manuscript).

We have begun to develop a systematic methodology to compare spatial with temporal variability in physical, chemical, and biological parameters of the LTER lakes. Comparison of variability patterns among parameters requires the development of a metric for spatial and temporal variability. Such a metric should be 1) parameter general, so that variability of diverse sets of parameters can be compared with a single metric, 2) scale dependent, because potentially the most interesting results will indicate how patterns of variability shift as temporal and spatial scale broaden or narrow, and 3) ecosystem general, so that different ecosystems can be compared and contrasted without bias. We are exploring this idea through the analyses of multiyear, multilake zooplankton data collected by Birge and Juday (Kratz et al. manuscript, section V) where we suggest that the ratio of temporal and spatial variability may be an appropriate metric (section V).

3. PROPOSED RESEARCH

Much of our research described above has theoretical and theory testing components. A program as robust as LTER has implications to many different approaches to ecological science. We present below only two of the sets of ideas we think are useful for us to pursue in the next five years.

a. A Metric for Temporal and Spatial Variability in Ecosystems

Some initial questions are:

1) In different ecosystems are the same types of components similar in respect to temporal versus spatial variability?

2) Are there any consistent patterns in the relations between temporal and spatial variation, and if so what do they mean?

We are developing parameters or metrics to compare temporal-spatial variability that is ecosystem general and provides information in interpretation of long-term, landscape ecology. Our next step is to apply the metric developed for zooplankton population and distribution data to other trophic levels as well as to chemical and physical parameters of the LTER lakes. The ratio of temporal to spatial variability will be compared for different components of lake ecosystems. To test the hypothesis further we will initiate intersite research with interested investigators at other sites to compare variability of components that appear different among ecosystems, but by function or analogy are at similar levels.

b. Problems of Scale: a Special Role of LTER

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). The existence of LTER attests to the groundswell of concern for scale in that it is itself a time scale defined program. Hierarchy theory provides a particularly useful conceptual framework for LTER because 1) it contains a coherent view of the nature of ecological complexity, 2) it explicitly analyzes the role of scale (the extent and grain of the observation set) in long-term observation, and 3) it can generate unifying principles for the entire LTER program because all 11 LTER sites study systems with multiple scales. The value of hierarchy theory thusfar in ecology has been principally as a post hoc model to clarify what has already been done. But it is a theory and as such it makes predictions that can and should be tested. We propose to derive and test predictions from explicitly stated principles of hierarchy theory.

It has been asserted (Allen et al. 1984) that the complexity of ecological systems derives from scale considerations. A complex system is one that requires several levels of organization for its adequate description. A special role of LTER in research into the nature of ecological complexity comes in principle from the long time periods that characterize the studies; since upper levels operate over long time periods, there is room for many lower ecological levels of organization with their short periodicities to exist inside the studies' purviews. Upper levels are characterized by relatively slow behavior and are the context of lower levels. The separation of levels is a separation in frequency of behavior. Hierarchy theory asserts the principle that complexity arises because of interference between fast and slow behaviors when entities from different levels interact.

Our first task in applying hierarchy theory will be to derive testable predictions from such principles. We would, for example, predict that the biomass of plankton would have a simpler frequency spectrum and be less dominated by higher statistical moments, like skewness, when rotifers are the main zooplankters than when copepods dominate. This is because rotifers have generation times that are relatively similar to phytoplankton division rates in comparison with copepods which reproduce much more slowly. Examples of other principles that are potentially testable across LTER sites are: 1) higher levels of organization may emerge through incorporation of disturbances of lower levels, and 2) a landscape is a higher level of organization than its equivalent community in that it holds the community out of equilibrium, a characteristic of higher levels in a hierarchy.

With LTER we are faced with many levels of organization, particularly the upper levels with which we have only limited experience. The hierarchical approach will not only test a burgeoning body of theory, but it will allow us to perform the more traditional analyses on the especially large systems that LTER demands, but with confidence that we have given the scaling problems proper attention. Macrolevel scaling is something that all the 11 LTER sites have to face, and so we consider hierarchy theory to be an important part of our intersite commitment. Tim Allen will lead this effort with the involvement of R. O'Neill of Oak Ridge National Laboratory who is on our Scientific Advisory Committee.

III. INTERSITE RESEARCH AND RELATED PROJECTS

Intersite research has been indicated throughout the previous sections of our proposal and is tied to the research work questions at our own site. Below we briefly highlight several of our intersite projects.

A. TEMPORARY LAKES AT JORNADA

Northern Lakes personnel are working closely with researchers at the Jornada site in investigation of the limnology of a playa lake. This temporary aquatic habitat filled twice in 1984 after an eleven year dry period. Research to date has revealed that 1) groundwater rather than evaporation accounts for the major water losses, 2) extremely high concentrations of potassium in playa waters probably result from leaching from vegetation washed into the basin, and 3) high populations of crustaceans develop almost immediately after playa flooding but predation by amphibians markedly reduces the numbers of some species. Bowser and Frost are continuing collaborative efforts with the Jornada group.

B. DISTURBANCE

Intersite work on disturbance presently stresses conceptual issues and temporary pond ecosystems. The LTER intersite workshop on disturbance led to an examination of disturbances in lakes (Frost and Kratz, manuscript) and of the disturbance concept in general (Frost and White, manuscript). Ongoing work on community processes in temporary pond ecosystems involves comparisons of playa lakes at the Jornada site with temporary ponds in northern Wisconsin. Frost and Kratz lead our effort.

C. CLIMATE PATTERN ANALYSIS

Extensive, comparable data are currently being collected for meteorological parameters at most LTER sites. In addition, most sites have detailed past records available on climate. Bowser and Robertson are collaborating with Jornada personnel in preparing an intersite workshop focusing on meteorological data. Computer communication links are being established to insure that comparable data bases will be available from all sites. More detailed comparisons among sites are expected to follow the workshop.

D. DATA MANAGEMENT

We have assigned a high priority to data management and personnel have been active in the related intersite activities. Although data system needs of each LTER are relatively unique, it has become increasingly apparent that similar management approaches at each site will foster intersite comparisons. We have been involved in developing general systems for data transfer among LTER sites. Abilities to communicate among sites will become increasingly important as data become more extensive and more emphasis is placed on intersite research. Benson and Bowser lead our effort.

E. SPATIAL/TEMPORAL VARIABILITY IN ECOSYSTEMS

Drawing on our experience with lakes, we are developing general approaches to compare temporal and spatial variability in ecosystems. We are developing parameters to compare temporal-spatial variability that are ecosystem independent. We will collaborate with investigators at other LTER sites to compare such parameters among ecosystems. Kratz will lead our effort.

F. THEORY TESTING AND DEVELOPMENT AT LANDSCAPE AND LONG-TERM SCALES

Hierarchy theory (Allen and Starr 1982, Allen et al. 1984) provides a conceptual approach that is appropriate at the scale of long-term ecological research and landscape ecology. We plan to develop testable hypotheses drawn from hierarchy concepts based primarily on our experiences with lakes and test them at other cooperating LTER sites. A possible example would be to rigorously examine similarities between the response to oxygen depletion beneath the ice of lakes (an oxidative process with community consequences (Tonn et al. 1983)) and the effects of fire on the prairie (an oxidative process with community consequences (Daubenmire 1968)). T. Allen will lead this effort.

G. SYMPOSIUM ON LONG-TERM ECOLOGY OF LAKES

We 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.

We will request funds for the symposium directly from NSF. Frost and Magnuson lead this effort.

H. AFFILIATED PROJECTS AT THE NORTHERN LAKES LTER SITE

LTER research activities have helped to attract an extensive number of research programs in aquatic ecology to the Northern Highlands area (Appendix 3). In many cases this research is conducted on our primary or secondary lakes and not only draws on extensive data available through our LTER research but also complements LTER activities. Examples range from development of acoustic technics, for examining fish biomass and distribution funded by ONR (Rudstam et al. manuscript), to ecological analyses of algal symbionts in freshwater sponges funded by NSF Ecology (Frost), to a multi-university study on predatory interaction between fish, snails, crayfish and other invertebrates along distinct environmental gradients funded by NSF Ecology (Lodge et al.), to the Little Rock Lake Environmental Acidification funded by EPA..

IV. MANAGEMENT AND ORGANIZATION

A. NORTHERN TEMPERATE LAKES LTER PROGRAM

Personnel, bibliographic information, and organizational management for our LTER site are provided in Appendix 7. In general, the Program Director (John J. Magnuson) with the assistance of the Deputy Director (Carl Bowser) have overall responsibility for program management and direction; they report to the Director of the Center for Limnology. Major scientific input on research goals and policy is provided by the Research Management Committee of principal investigators on the North Temperate Lakes LTER program. In addition, an External Scientific Advisory Committee group of accomplished scientists not directly associated with our LTER site which meets every other year to provide constructive criticism. They were very helpful in year one-five. The Site Manager (Timothy Kratz) oversees regular sampling, supervises technicians and works with the Deputy Director in the supervision of data management. Support Staff assist the Director with fiscal, personnel, and clerical activities.

Technicians conduct most field work and sample processing. The Data Manager (Barbara Benson) has responsibilities for the reduction, storage, and retrieval of data and also supervises a part-time museum curator. Research Programs are the individual investigator research activities closely linked to or supported by LTER.

B. THE CENTER FOR LIMNOLOGY

Our LTER program on north temperate lakes is operated by the Center for Limnology at the University of Wisconsin, Madison. The Trout Lake Station is one of two laboratories in the Center; the other is the Limnology Laboratory on Lake Mendota. The Center was established as a research unit within the College of Letters and Sciences on July 1, 1982. Previously, the units of the Center were administered through the Zoology Department. Formation of the Center for Limnology reflected a need for a single research unit representing the interest of limnologically oriented faculty and researchers at the University of Wisconsin-Madison as well as for visiting researchers. The Center's formation was catalyzed in part by the choice of Wisconsin as the north temperate lake site for the LTER program.

The Center functions administratively with a Director, (John J. Magnuson), Associate Directors for the Trout Lake Station (Thomas M. Frost) and the Limnology Laboratory on Lake Mendota (James F. Kitchell), a Research Coordinator, Project Coordinator in Electronics, Data Manager, a Librarian, a Mechanician 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 of $181,889 in FY85, extramural funding of $1,100,025 (Appendix 8), Graduate School Development funds from the Wisconsin Alumni Research Foundation of $150,000 over a 5 year period, a Center for Limnology Endowment producing $7,500 for 1985, and capital equipment support from the University of $25,000-35,000 per year. Detail on University support for facilities and equipment is presented in Appendix 8). 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,

We strongly encourage the use of Center facilities by investigators from other institutions. Opportunities for use of the Center are presented through participation in scientific meetings and personal contacts. We also prepared an article (Magnuson and Frost 1982) on the Trout Lake Station in the Ecological Bulletin. Communication is working; EPA presently is using and DOE is considering using the Trout Lake Station for major long term ecological experiments on acid deposition. Numerous other projects are using or planning to use the site (Appendix 3).

C. TROUT LAKE STATION

1. INTRODUCTION

Owing partly to the catalytic effects of LTER, we have experienced a significant and rapid growth in research activity at Trout Lake from both Wisconsin and visiting researchers. In 1985 the number of research dollars focused on Trout Lake as a field site are approximately $590,000 from University of Wisconsin investigators and approximately $380,000 from visiting researchers. Other researchers continue to show interest owing to the level of research activity, the developing data base, and opportunities for collaborative research.

These developments have resulted in serious overcrowding and we have a proposal pending with NSF-Biological Resources Research to build an extension onto the main laboratory at the Trout Lake Station. In addition, the University is funding several new housing units to increase station capacity.

2. SITE DESCRIPTION

The Trout Lake Biological station serves as a research base for the Northern Highlands Lake District. This region, approximately 10,000 km^2, 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. 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 lakes. Other available conditions include: dimictic, meromictic and monomictic lakes; atmosphere dominated, groundwater dominated and drainage lakes; lakes with varved sediments, winterkill lakes, temporary and permanent forest ponds, and reservoirs. Lakes are usually ice covered from late November to late April.

The district is also the source area for major river systems such as the Wisconsin and Flambeau of the Mississippi system, the Brule and Menominee flowing into Lake Michigan, and Presque Isle flowing into Lake Superior. Within a 10 km radius of the Station there are approximately 60 km of streams. Vilas County has approximately 640 km of streams, not counting the numerous intermittent streams.

Lakes within the Northern Highlands exhibit near natural water quality conditions. 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. Outdoor recreation and forestry form the economic base for the 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 $5^{o}C$. 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.

3. FACILITIES

The all-season laboratory is a two story structure 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. Additional space is dedicated to offices, instruments, aquaria and a library. 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 aquarium and incubation rooms. An auxiliary power plant is available at the station.

Five service buildings at the station provide facilities for equipment and vehicle storage.

Year-round housing at the station can accommodate 14 people. Seasonal facilities provide space for an additional 12 persons during peak activity periods. Two new three season cabins (suitable for 3 people each) are under construction and 2 more are planned for 6 more persons. When completed, total capacity would be 14 in winter, 26 in spring and fall and 38 in summer. 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: four trucks, three large and two small boat trailers, a ski barge, five Arkansas traveler workboats, seven alumnicraft 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, plankton samplers, trawls, fyke nets, gill nets, seines and an electroshocking boat.

Our laboratories are equipped with fume hoods, a millipore reverse-osmosis and milli-Q water purification system, drying oven, muffle furnace, dry sterilizers, temperature controlled incubator, balances, a UV-visible dual beam spectrophotometer, autotitrator for alkalinity, and Beckman models LS 1801 liquid scintillator counter. Available microscopes include: a Zeiss Inverted Microscope equipped for epiflourescence, Nikon Labophot microscope, and 3 Wild model M5A dissecting scopes. The laboratory has several large fiberglass holding tanks, four 75-gallon fiberglass aquaria and assorted small aquaria. Data entry and analyses as well as word processing capabilities are provided by 2 Apple IIe microcomputers and a letter quality printer.

D. LIMNOLOGY LABORATORY

The Laboratory of Limnology on the Madison campus serves as the administrative base of north temperate lakes LTER and the Trout Lake Station and is the field station for Lake Mendota research. Several principal investigators on LTER are located here or in the Botany Department.

E. GEOCHEMISTRY LABORATORY

Chemical analyses for lake and groundwater monitoring are performed in the geochemistry laboratory in the Department of Geology and Geophysics. Analyses are conducted by a full time specialist with the assistance of hourly helpers. Analyses, data reduction, and logging, of preparation of reagents, standards, and ultra-clean sampling bottles, and oversight of supply needs for both the geochemistry laboratory and the Trout Lake chemistry laboratory are all part of the specialist's responsibilities. Technic selection, quality control criteria, and specific sampling/analytical procedures are determined by the PI's experienced with analytical chemistry (Armstrong and Bowser) in collaboration with the chemical specialist.

F. WATER CHEMISTRY LABORATORY

The Water Chemistry Laboratory, located on Lake Mendota 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.

G. THE UNIVERSITY OF WISCONSIN 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. We plan to develop with the Museum a laboratory for counting plankton in the future. Counting is presently done at Trout Lake but facilities there are at a premium for field research. The Zoological Museum provides a safe and professional repository for long-term research collections for aquatic ecology and limnology. Dr. Kirsch has a proposal pending with NSF's Biological Research Resources Program for much needed developments to meet the needs of LTER and other limnological research.

H. COMPUTING FACILITIES

The LTER computional facilities presently use seven LTER and five other microcomputers at several sites on the Madison campus and at the Trout Lake Station as well as a Sperry UNIVAC 1180 and VAX 780 at the Madison Area Computing Center (MACC).

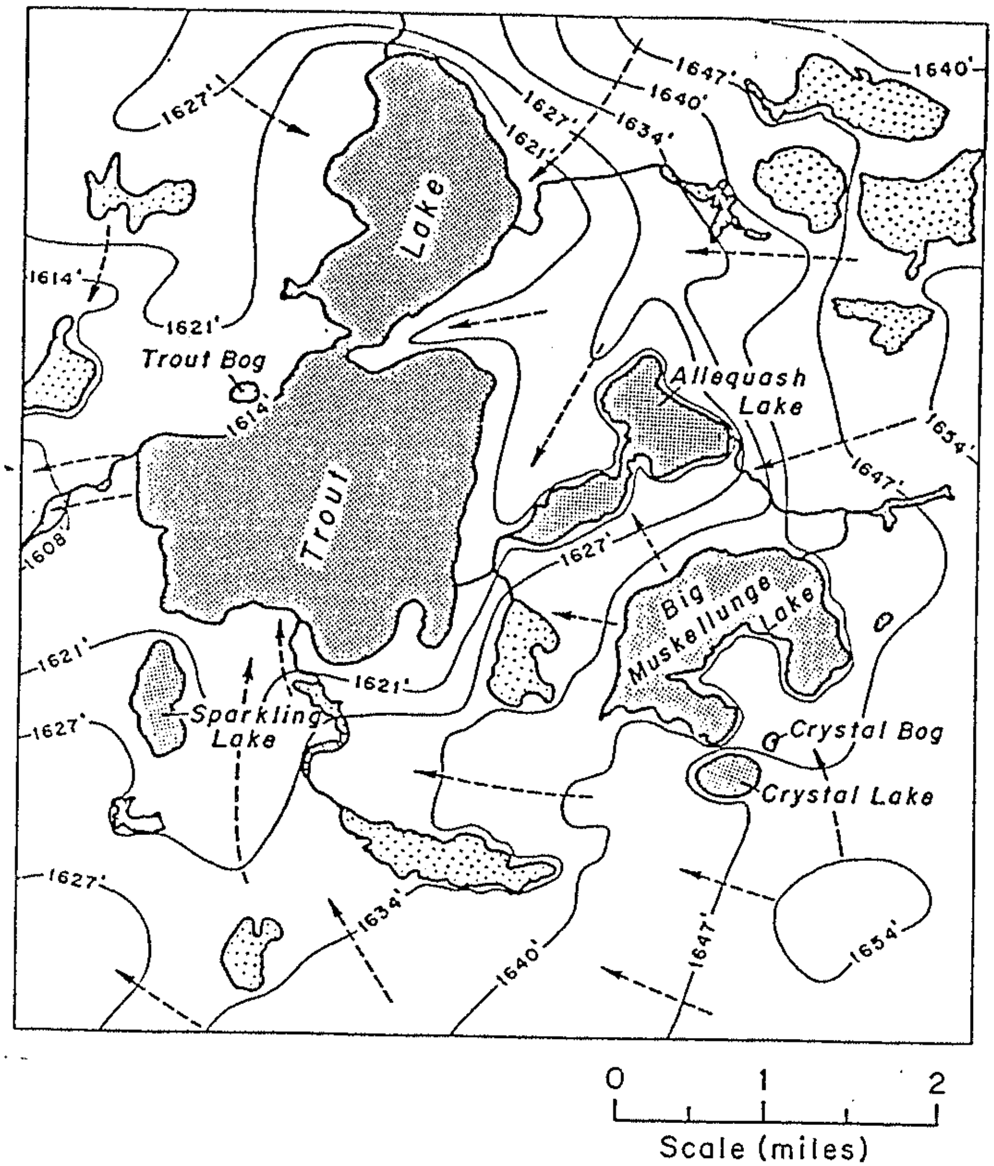


Figure 1. LTER primary lakes (fine stippling and named) at the north temperate lake site, along with water table elevations (contours in feet) and direction of groundwater flow (arrows) (Okwueze 1983)

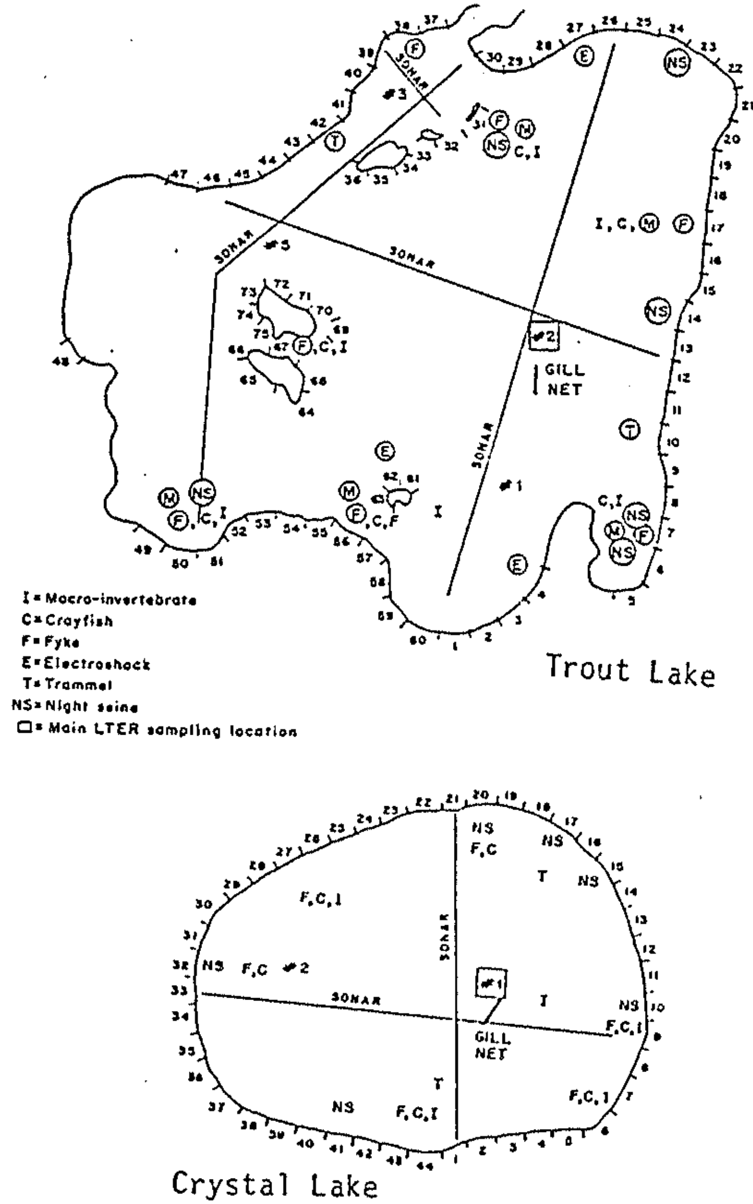


Figure 2. Sampling sites for two of the seven primary LTER lakes at the north temperate lake site.

Table 1. Descriptive physical, chemical and biological features of the primary lakes of the North Temperate Lakes LTER Program

	LAKES (arranged by order in the groundwater system)					BOG LAKES	
	CRYSTAL	SPARKLING	BIG MUSKELLUNGE	ALLEQUASH	TROUT	CRYSTAL BOG	TROUT BOG
Area (ha)	3.6654 x10	8.1385 x10	3.9634 $x10^2$	1.6545 $x10^2$	1.6079 $x10^3$	1.0	2.0
Max. depth (m)	20.4	20.0	21.4	7.6	35.7	2.5	7.5
Mean depth (m)	10.37	10.87	7.54	2.92	14.62	2.0	6.0
Shoreline length (km)[a]	2.3	4.3	14.5	9.5	25.9		
Ave. length of ice cover (days)[b]	143	145	145	152	143	155	160
Mean winter temperature (°C)[c]	2.9	2.9	2.2	2.1	1.9	3.1	2.6
Thermocline depth (m)[d]	8.1	7.3	9.3	5.3	10.3	none	2.1
Mean summer epilimnion temperature (°C)[e]	21.1	21.2	21.2	21.6	19.7	21.5	20.8
Mean summer hypolimnion temperature (°C)[f]	8.2	5.9	8.8	none	5.9	none	4.5
Mean summer secchi (m)[g]	8.3	6.6	7.2	3.0	4.6	1.4	1.2
Mean summer extinction coefficient[h]	.200	.336	.317	.797	.376	2.165	1.845
Minimum depth summer anoxia (m)[i]	not anoxic	16	15	5	32	2	2
pH[j]	5.72	7.14	7.07	7.29	7.41	4.82	4.55
Conductivity (spring mixis) (umhos/cm)[k]	14	72	43	82	85	12	20
Alkalinity (ueq)[j]	6	571	339	742	808	1	-8
Total P (spring mixis) (filtered, ug/l)[l]	2.3	3.9	2.8	8.4	2.0	5.8	4.0
SiO_2 - Si (spring mixis) (ug/l)[k]	2	3624	150	6036	4134	298	507
Cl (ppm)[j]	0.45	2.64	0.53	0.31	1.33	0.17	0.29
SO_4 (ppm)[j]	3.68	3.25	3.24	3.45	3.07	1.41	2.93
Ca (ppm)[j]	1.1	8.8	5.2	10.6	11.7	0.63	1.34
Mg (ppm)[j]	0.25	2.55	1.67	2.91	3.01	0.23	0.40
Mean summer chlorophyll (ug/l)[m]	1.1	1.1	1.7	3.8	1.6	4.5	8.6
# fish species[n]	8	17	27	25	33	1	3

a Juday and Birge (1941); Black et. al (1963)

b Fall 1981-Spring 1984

c The volumetric mean average temperature from January 1 to March 30, 1982-83 (three temperature profiles per year).

d The mid-point of the metalimnion defined by Wetzel (1983); determined from the average temperature profile from June 15 to August 15, 1981-84 (five temperature profiles per year).

e The average temperature at 1 meter from June 1 to August 31, 1981-84 (six temperature profiles per year).

f The average temperature 2 meters above the maximum lake depth from June 1 to August 31, 1981-84 (six temperature profiles per year).

g Average value 1982-83 from June 1 to August 31.

h Average value 1981-83 from June 1 to August 31.

i Minimum depth 1982-83 at which the oxygen concentration was less than or equal to 0.5ppm in the period June 1 to August 31.

j Weighted average of spring and fall mixis values 1981-83.

k Average surface-most value 1982-83 at spring mixis.

l 1983 surface-most value at spring mixis.

m Average surface value 1982-84 from June 1 to August 31.

n Cumulative number present 1981-83.

Table 2. Sampling scheme for the 7 primary lakes at the North Temperate Lakes LTER Site

PARAMETER	FREQUENCY	LOCATION	METHOD
WEATHER (1)(2) Air Temperature Relative Humidity Precipitation	Daily	Trout Lake Station Grounds	Max-min thermometer Hygrothermograph Standard Precipitation Guage
PHYSICAL/CHEMICAL LIMNOLOGY Water Temperature Light, Secchi Disk Dissolved Oxygen Conductivity	Bi-weekly during ice-free season; monthly during ice-covered season	Deep hole of each lake; measured at meter intervals	Measured in situ with Montedoro-Whitney DOR-2A, CTU-3B and/or YSI 57. Light measured with Licor 858 quantum sensor
pH Chlorophyll a, Phaeopigments NO_2-N, NO_3-N, NH_4-N, SiO_2-Si		Deep hole each lake: samples at top and bottom of epilimnion mid-thermocline, and top, middle and bottom of hypolimnion	Samples taken with peristaltic pump, with Analyses in lab
Total Dissolved P Major Cations: SO_4-S CL- Alkalinity	- spring and fall mixing - winter and summer maximum stratification		Samples taken with peristalic pump with in line filtration. Analyses in lab
Ice thickness snow depth on lake	Monthly or bi-monthly in winter	Ice thickness at deep hole--snow depths at random locations	meter stick
PLANKTON Zooplankton	Three bi-weekly samples during overturn, and maximum summer stratification, monthly to bi-monthly at other times	Deep hole of each lake. 2-7 depths per lake using per lake using same depths as Birge and Juday. Vertical tow.	Schindler-Patalas Trap Wisconsin Net 80mm mesh
Phytoplankton		Deep hole of each lake. Integrated total water column sample during mixing: separate epi-, meta- and hypolimnetic samples during stratification	Peristalic pump with weighted Tygon tubing
Phytoplanktanic primary production			In lab C-14 incubation under controlled light and temperature
FISH	Annually, in August	Gill Nets: Deep Hole, Fyke, Trammel Seine - at selected reference stations Sonar: Transects	Vertical Gill Nets, Fyke Nets, Trammel Nets, Seines, Electro boom shocker, Sonar Transects 70 kHz vertical sounder
BENTHOS Crayfish	Annually in August	At Fyke Net Stations	Cylindrical Crayfish Traps baited with beef liver
Deep Water Shallow Water	Annually, in August and September	Deep Hole of each lake and at Fyke Net Stations	Conical Net vertical tows for Mysis and chauborus. 'Dendy' samplers for others. Hand collect clams
MACROPHYTES Distribution:	Once per lake	Entire lake	line transect
Biomass:	Annually	Fyke Net Stations in selected lakes	line transect
GROUNDWATER Level Temperature	Monthly	89 samplers from east of Crystal Lake to Trout Lake	Nests of piezometers, chemistry methods same as for lakes
Dissolved Oxygen pH, Alkalinity, Ca^{++}, Mg^{++}, Na^{++}, K^{+}, Cl^{-}, SO_4, Iron, Silicon	Quarterly		

(1) National Atmospheric Deposition site is also located on Trout Lake and maintained by the Wisconsin Department of Natural Resources:

(2) Seven other atmospheric monitoring sites are located within 50 km of the Trout Lake Station with continuous records as early as 1903 (see appendix 2).

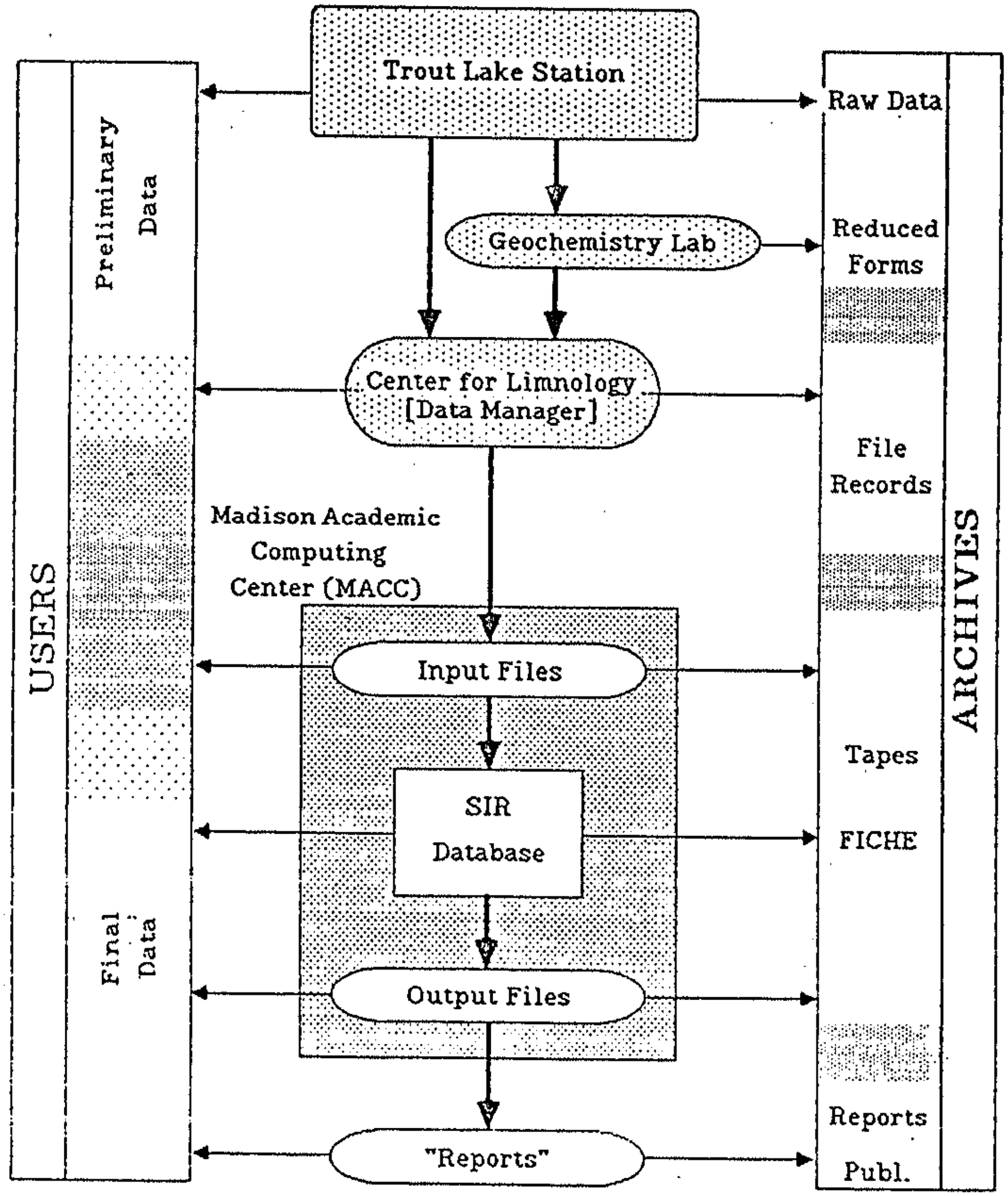


Figure 3. Flow scheme for data at the North Temperate Lakes LTER site.

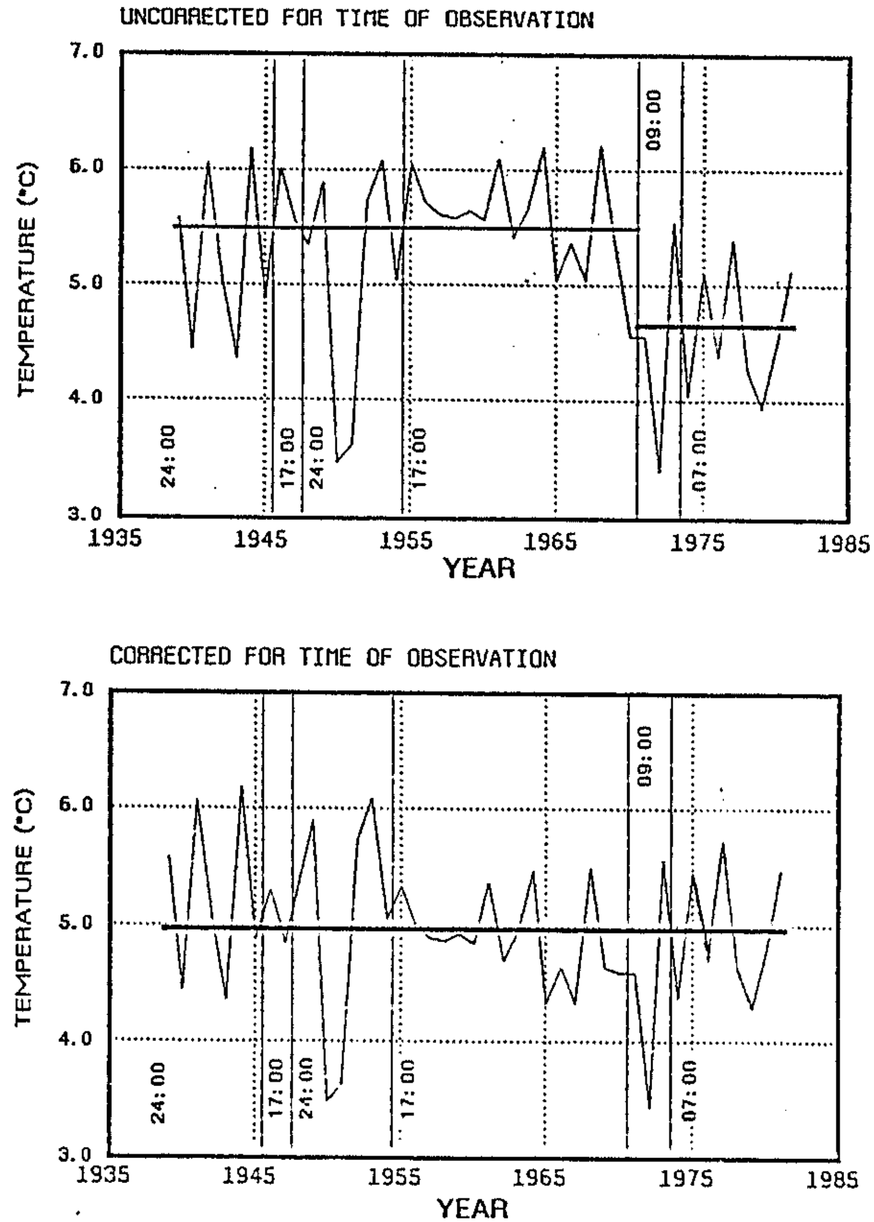
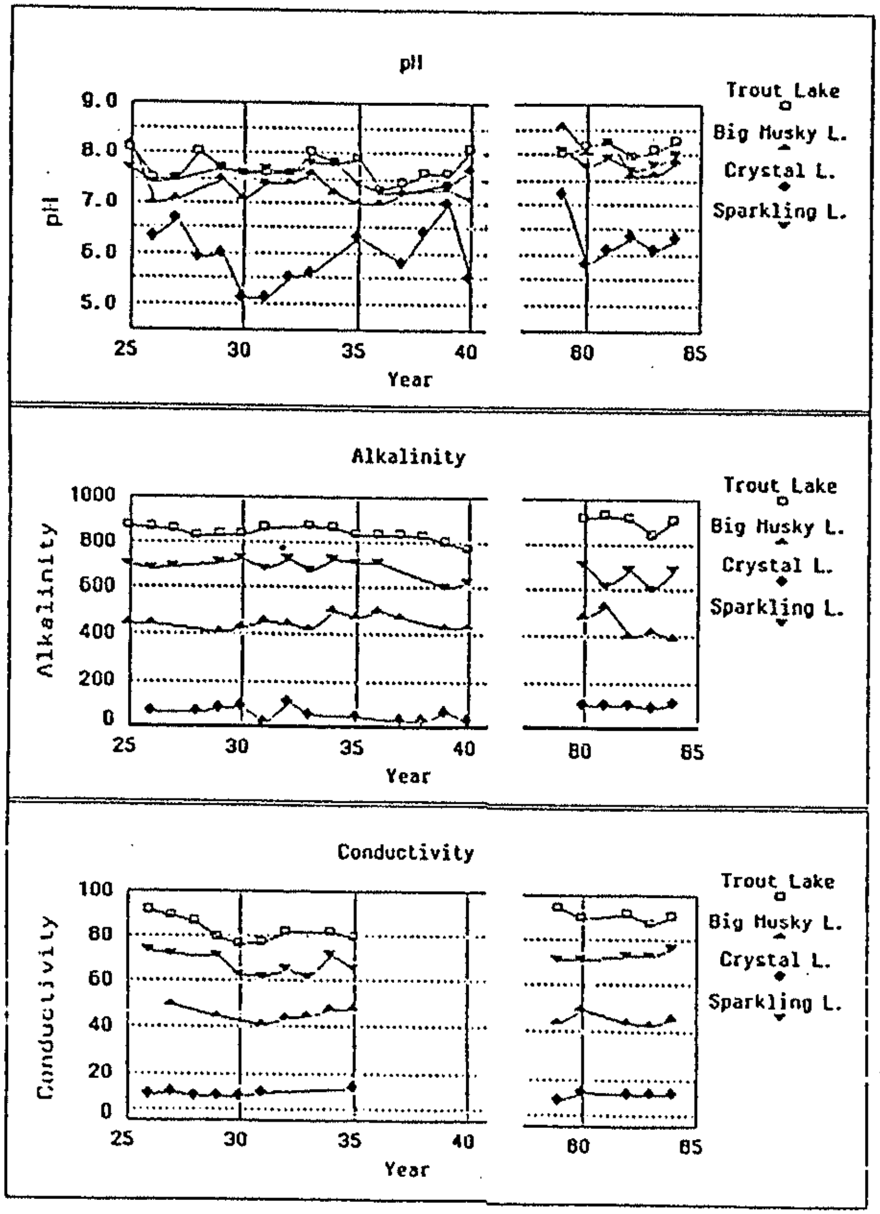


Figure 4. Time course for mean daily temperatures showing the effect of time-of-day corrections on measurements.



Lake	pH historic	pH recent	P
Crystal	5.9	6.3	NS
Big Muskellunge	7.3	8.0	*
Sparkling	7.5	7.9	*
Trout	7.7	8.1	*

Lake	Alkalinity historic	Alkalinity recent	P
Crystal	0.06	0.10	*
Big Muskellunge	0.45	0.45	NS
Sparkling	0.69	0.66	NS
Trout	0.84	0.90	*

Lake	Conductivity historic	Conductivity recent	P
Crystal	11	13	*
Big Muskellunge	46	45	NS
Sparkling	68	73	*
Trout	82	91	*

Figure 5. Change in laboratory pH, conductivity, and alkalinity of surface water for four LTER lakes for which sufficient historical data (1925-41 Univ. Wisconsin Archives) are available to compare with recent data (1979-84 LTER North Temperate Lakes Data Base). * significant at $P \leq 0.05$ with a two tailed t-test. Sample size of water chemistry measurements/lake: historic = 7 to 16 years; recent = 5 to 6 years.

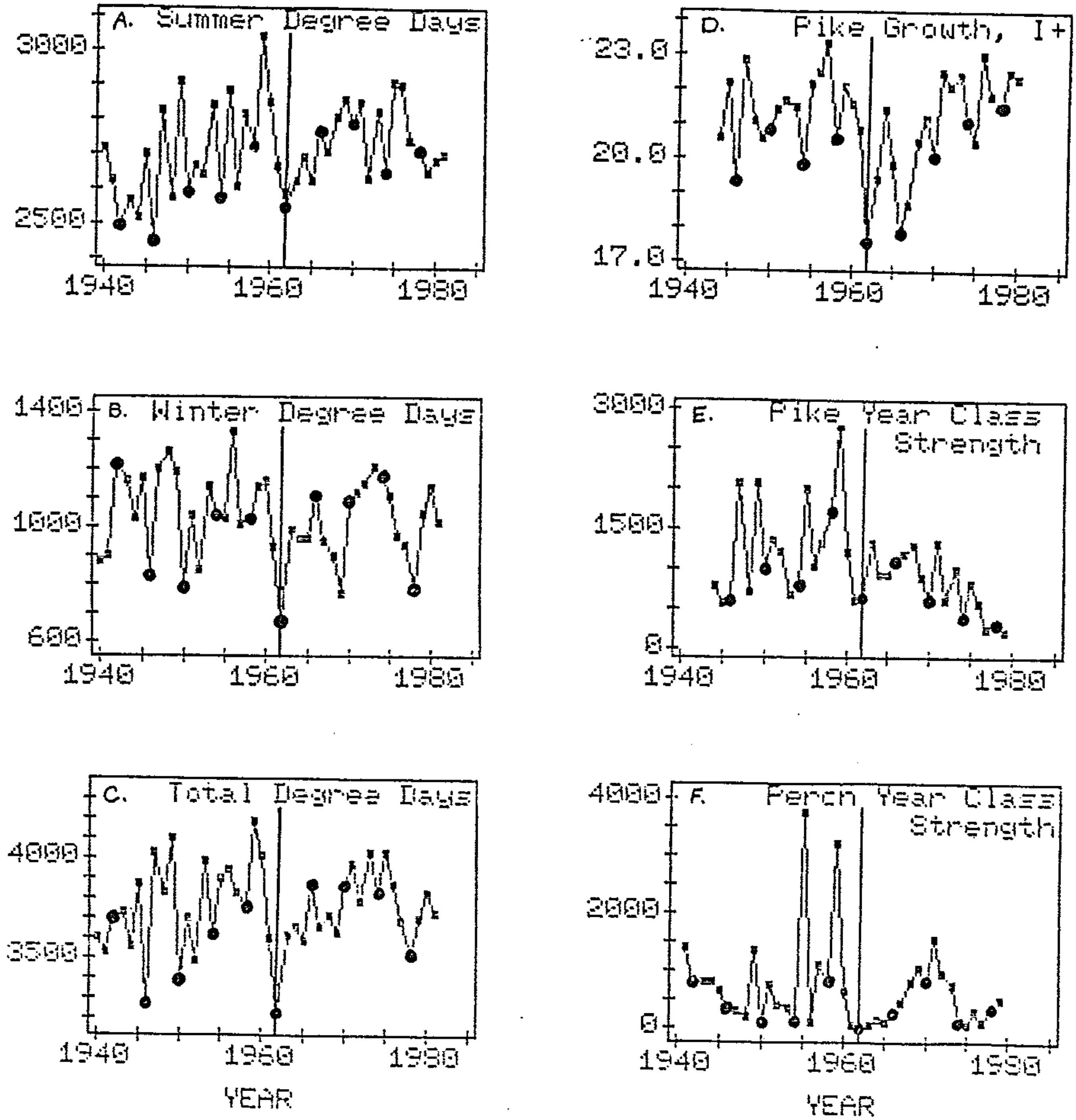


Figure 6. Long-term data on yearling pike growth (D) and related parameters from Lake Windermere UK in the same calendar years. Dark circles indicate four year interval with poor yearling pike growth.

Table 3 Silica and water fluxes in Crystal Lake (May 1982 to May 1983).

Flux	Silica: Total amount (kg year^{-1})	Silica: DRS content (mg liter^{-1})	Water (10^3 m^3 year^{-1})
	Inputs		
Ground water	125 to 300*	4.9 to 7.4	21 to 39
Atmosphere (wet and dry)	0.7	0.002	346
Gross regeneration	200 to 510†		
	Outputs		
Ground water	1.3	0.010	127
Sedimentation‡			
Gross	380 to 570		
Net	200 to 375		

*See (*8, 13*). †Calculated from Eq. 1. ‡Gross sedimentation refers to the flux of settling PBS as measured with sediment traps (*9*). Net sedimentation refers to PBS permanently accumulated in the bottom sediments (*10*).

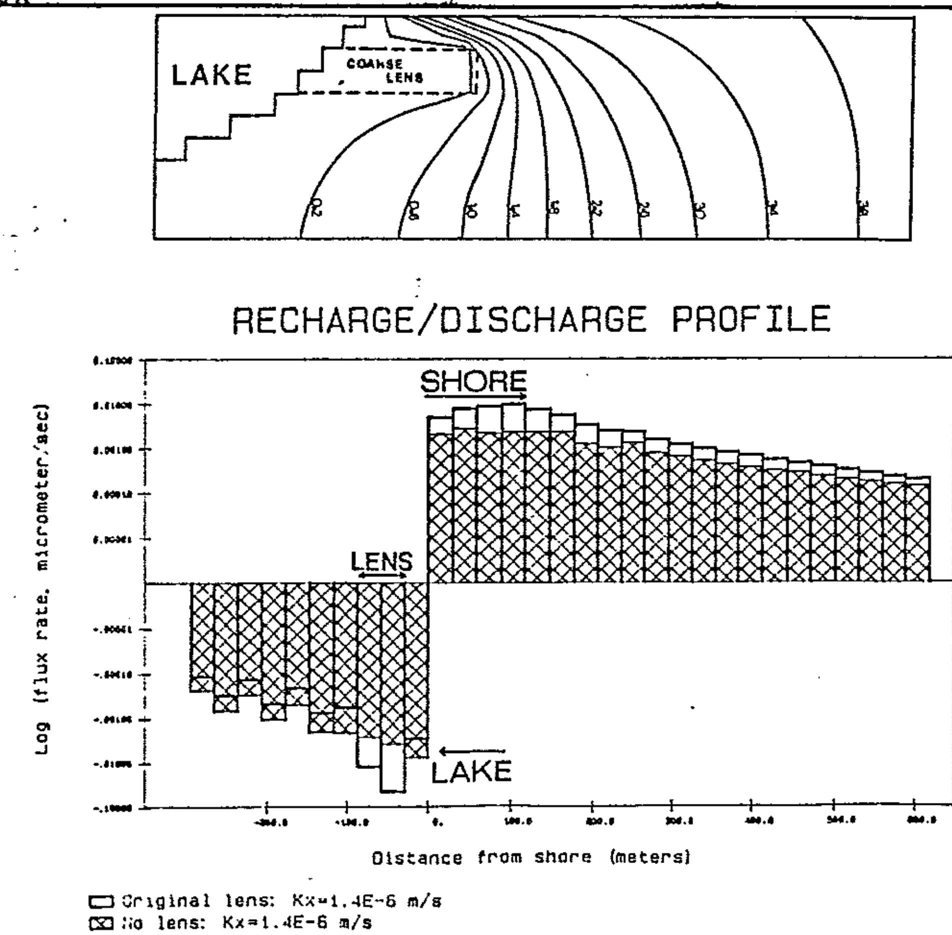


Figure 7. Groundwater discharge models showing the effects of a coarse gravel lens on flow near Trout Lake. Negative values indicate discharge to the lake. A model incorporating a coarse lens provides the closest match to field conditions.

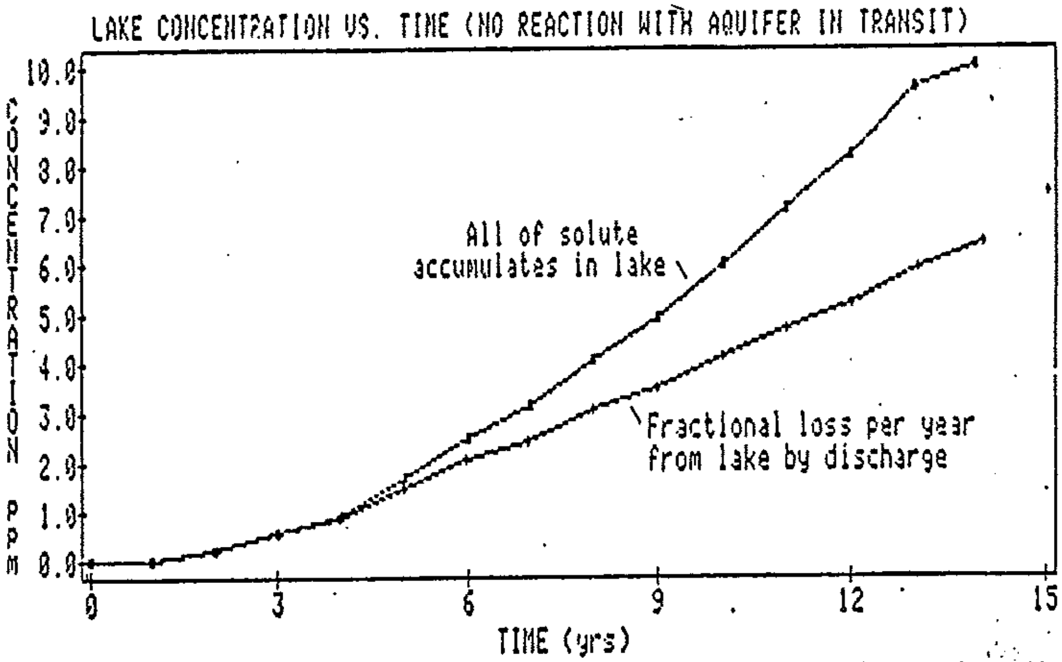


Figure 8. Time course of the accumulation of a solute in a lake after transport is buffered by groundwater flow.

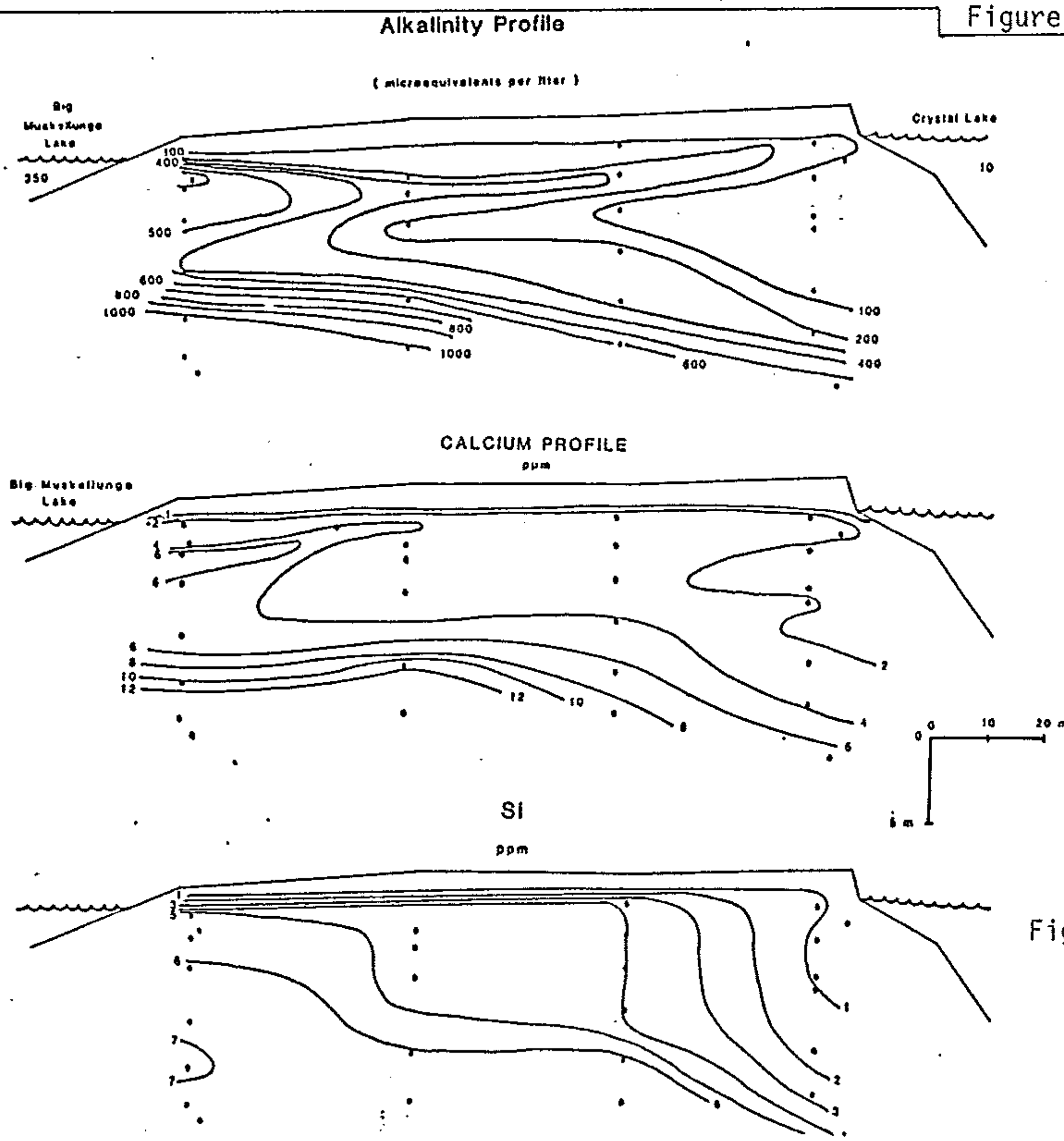


Fig. 9. Chemical characteristics of groundwater flowing from Crystal Lake (l) to Big Muskellunge Lake (r).

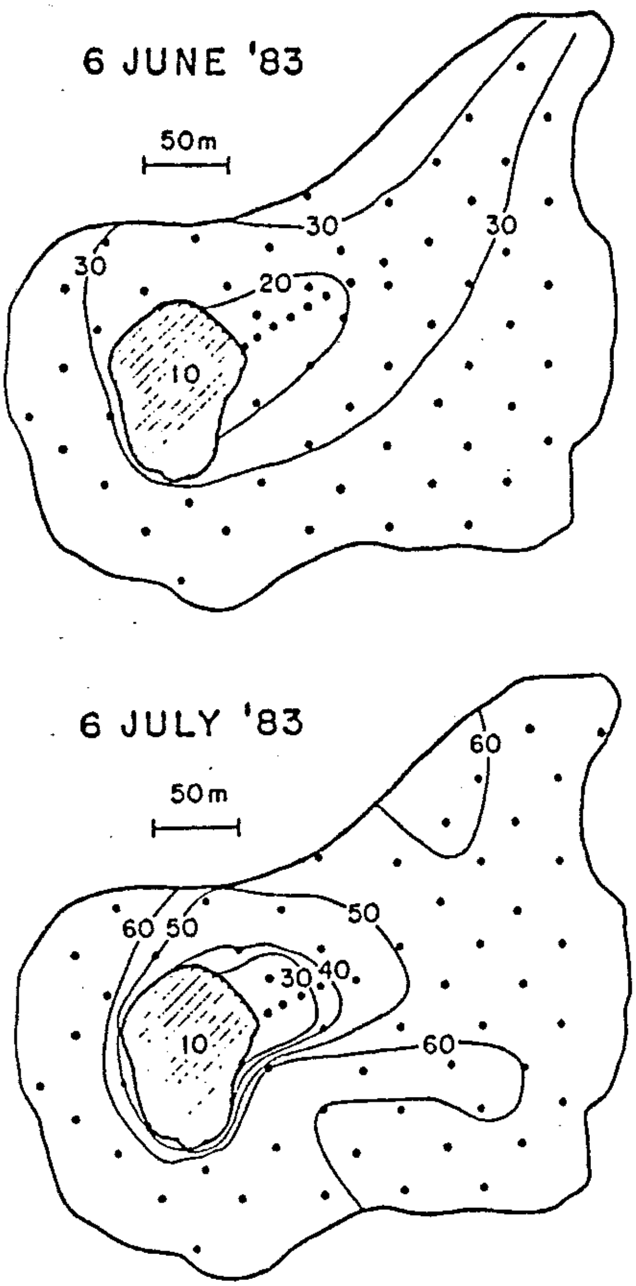


Figure 10. Conductivity (μSi/cm) in shallow groundwater surrounding Crystal Bog.

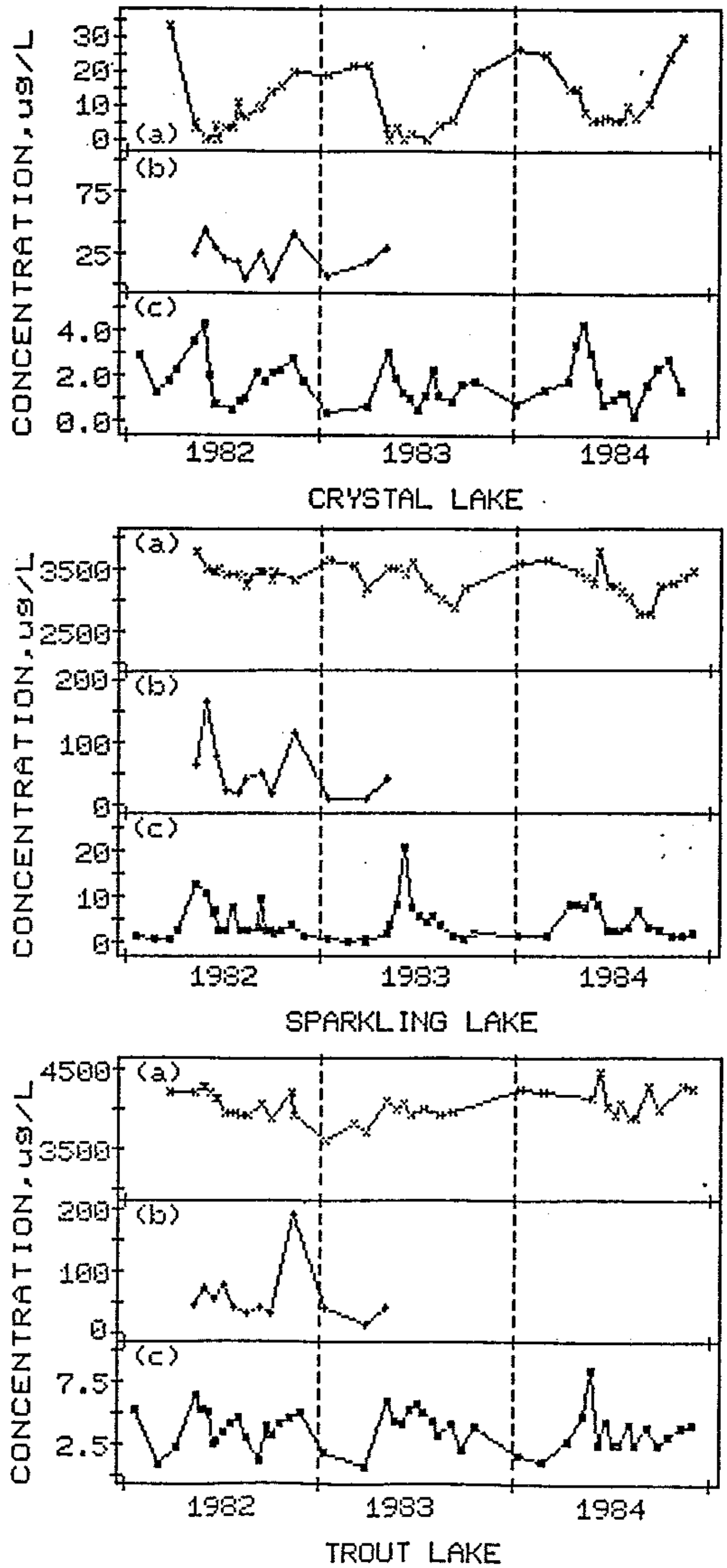


Figure 11. Concentrations of (a) dissolved reactive silica, (b) biogenic, particulate silica, and (c) chlorophyll a in water at 8 - 12m depth in Crystal, Sparkling and Trout Lakes.

Table 4. Changes in the abundance (catch/24 hr. gillnet set) of pelagic fishes in 4 LTER lakes, 1981-83 (n = two 24-hr sets/year with 19, 25, 32, 38, 51, 64, and 89 mm stretch mesh)

Lake	Species	1981	1982	1983	1984
Trout	Cisco	86	127	294	524
Big Muskellunge	Cisco	96	6	0	1
	Yellow Perch	157	0	0	0
	Walleye	2	1	12	12
Sparkling	Cisco	60	32	8	6
	Rainbow Smelt	0	6	4	56
	Walleye	2	0	1	2
Crystal	Yellow Perch	43	22	412	111
	Lake Trout	4	1	0	0

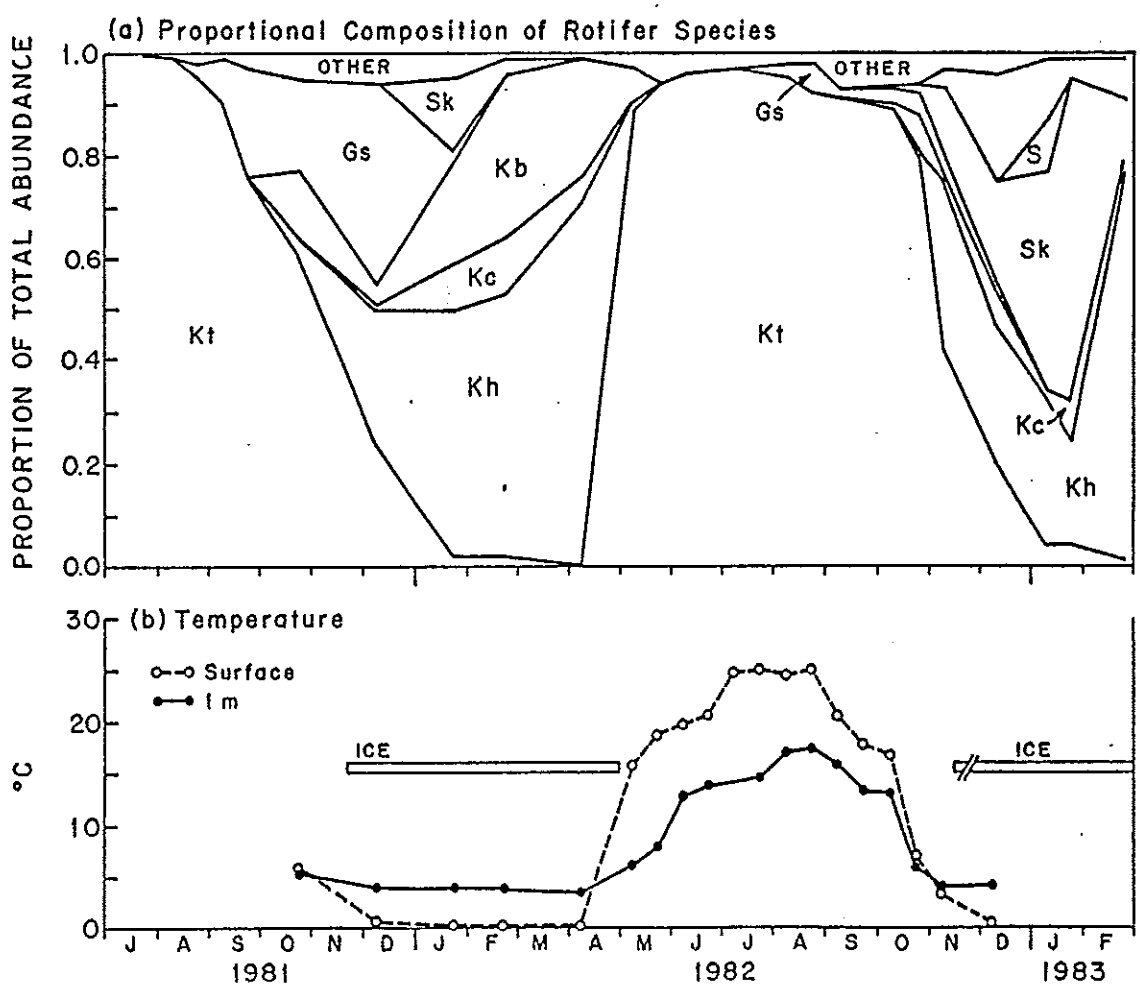
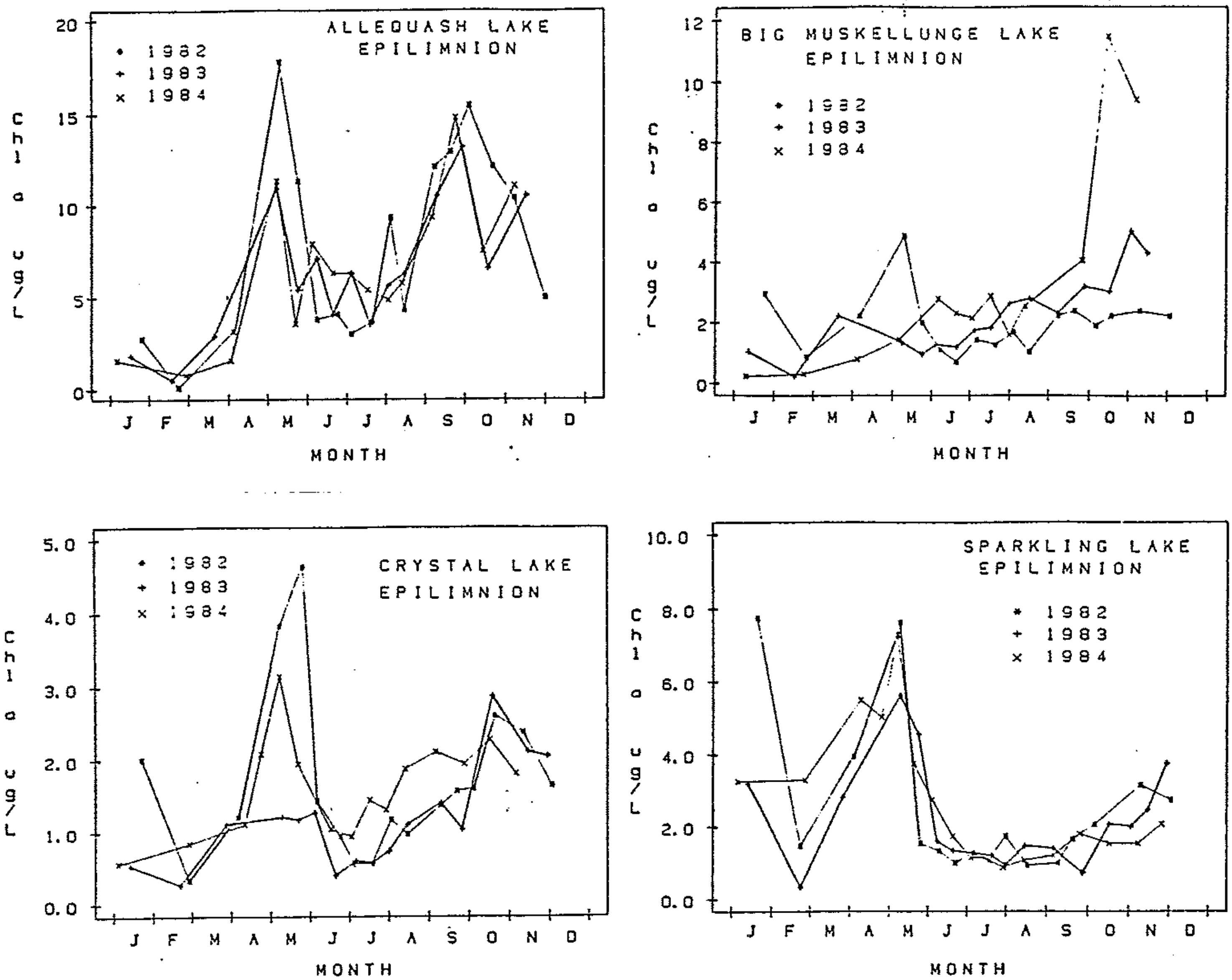


Figure 12. Relative abundance of rotifer species and temperature in Crystal Bog. Kt = Keratella taurocephala; Kc = K. cochlearis; Kh = K. hiemalis; Kb = Kellicottia bostoniensis; Gs = Gastropus sp.; Sk = Synchaeta sp.1. and S = Synchaeta sp.2.



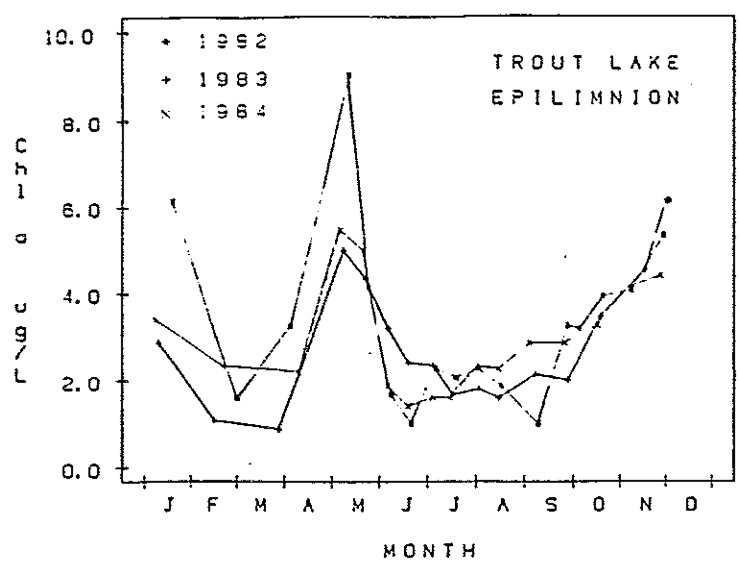


Figure 13. Mean epilimnetic chlorophyll a concentrations for three years in five, primary LTER lakes.

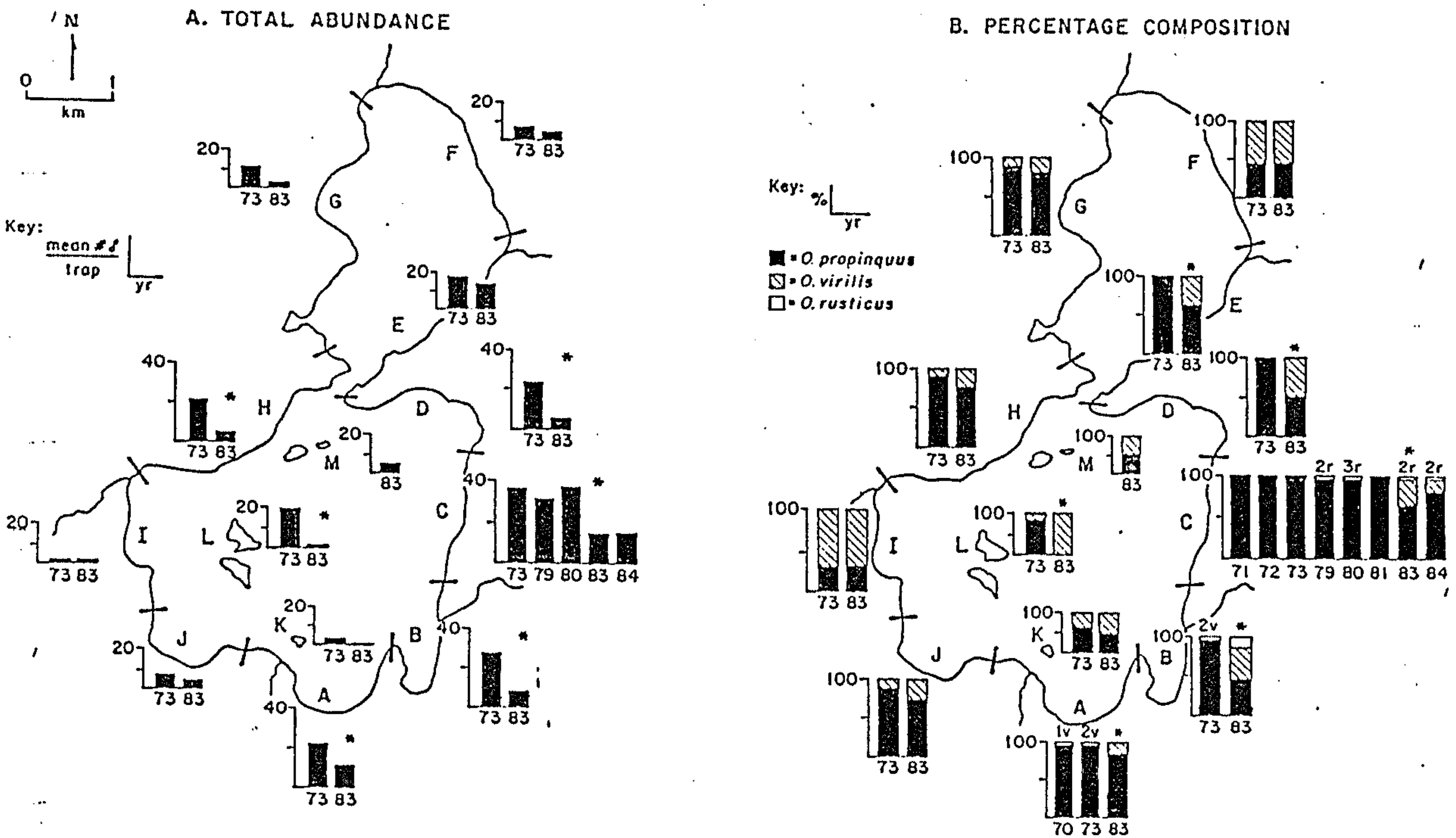


Figure 14. The abundance of all species combined (A) and percentage species composition (B) of Orconectes male crayfishes for shoreline segments (designated with capital letters) in Trout Lake during the period 1970-1984. Significant differences (P<0.05) in total crayfish abundance and in percentage species composition between 1973 and 1983 are noted (*). In B, very small percentages are given numerically above the histogram, e.g., "2r" denotes 2% O. rusticus, "2v" denotes 2% O. virilis. No 1973 data are available for segment M.

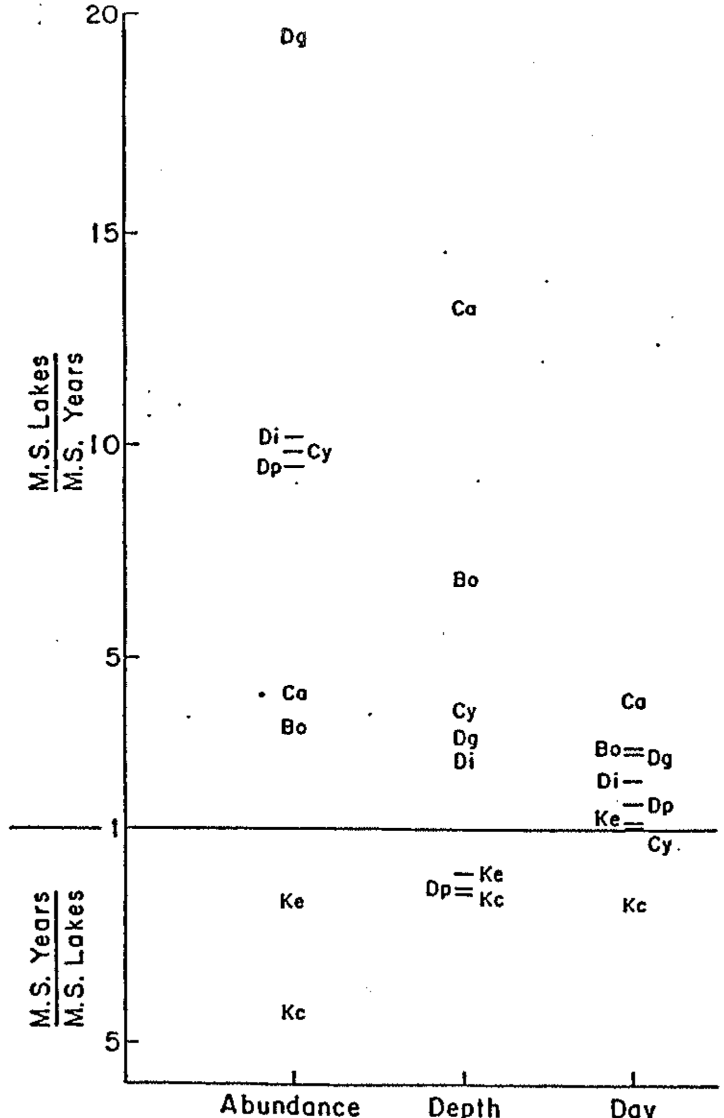


Figure 15. Ratios of mean square among lakes and mean square among years for maximum abundance, day and depth of maximum abundance of eight zooplankton taxa from five lakes in northern Wisconsin. Ca=Calanoid copepods; Cy=Cyclopoid copepods; Dg=Daphnia galeata mendotae; Dp=Daphnia pulex; Di=Diaphanosoma; Bo=Bosmina; Kc=Keratella cochlearis; Ke=Kellicottia. Ratios greater than 5 occurred less than 5% of the time in our null simulations, and therefore, are judged as indicating a significant association with a lake.

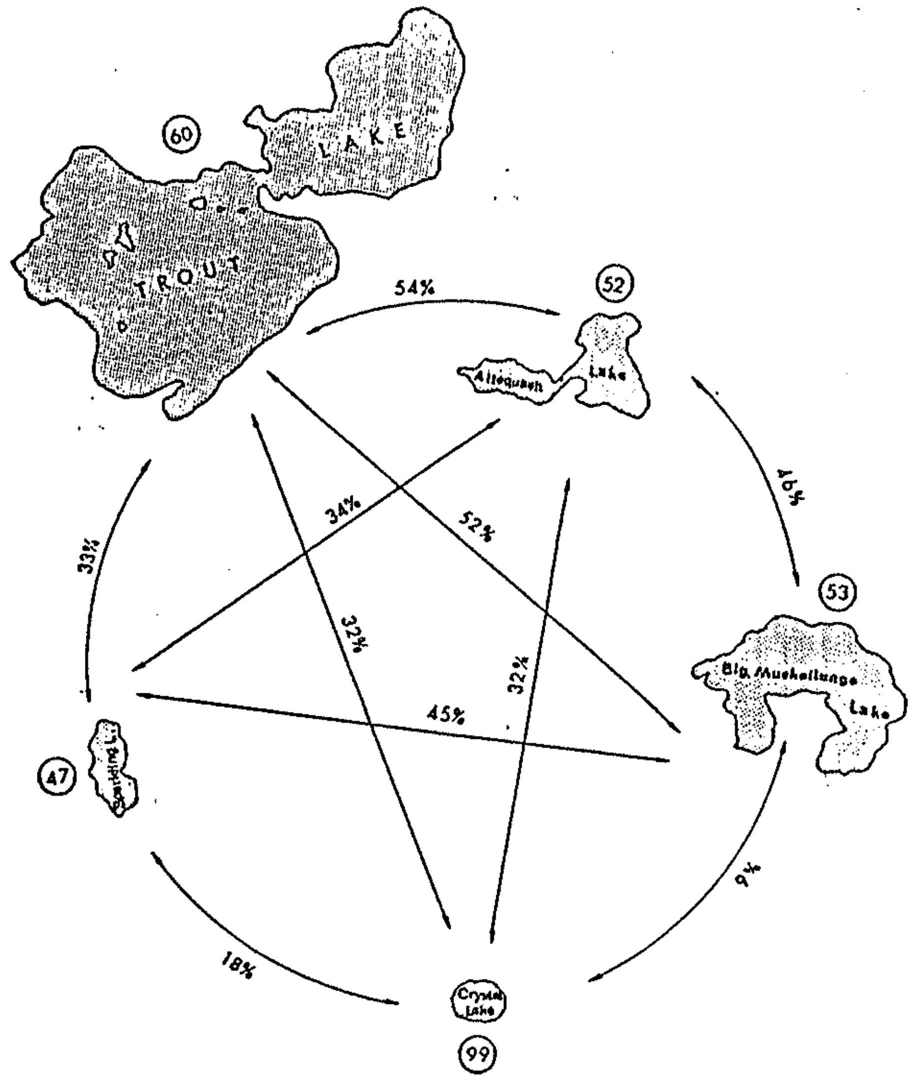


Figure 16. Percent similariries in littoral zone fish assemblages of LTER lakes based on percent species compositions. The index ranges from 0 to 100%. Circled values are the among year similarities for each lake over 3 years. Values on arrows between lakes are the among lake similarities based on a three year sample.

Appendicies

Appendix 1. References

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Appendix 2. Original List of Questions and Hypotheses in Addendum to Original LTER Proposal on the North Temperate Lakes, May 1980

A. What are the relations between climate and physical limnology of lakes?
   1. Lakes are effective climate indicators.
   2. Variations in climatic factors induce predictable variations in the thermal behavior of lakes from year to year.
   3. Meromictic properties of Mary Lake are changing in intensity in response to climatic and hydrologic factors.
B. How do year-to-year variations in precipitation affect the water chemistry in subsurface and surface water systems, and how do these in turn affect the phytoplankton?
   1. Year-to-year variations in precipitation will have their influence on lake chemistry via groundwater in the year in which the precipitation occurs.
   2. Groundwater is a major factor in the chemical budget of lakes.
   3. Annual differences in surface and groundwater inputs, via changes in water chemistry, will be reflected in the phytoplankton.
C. How do natural variations in wind, water budgets and heat budgets affect year-to-year stability in community structure of lakes through altered recruitment of consumer populations such as yellow perch and cisco?
   1. Year-to-year variations in climate determine recruitment of planktivorous fishes.
   2. Variations in recruitment significantly alter the structure of planktonic communities and nutrient cycling in predictable ways.
   3. Morphometric properties of lakes (volume and fetch) dampen weather induced variations in biotic structure of lake ecosystems.
D. What is the role of organic matter accumulation in controlling nutrient immobilization in lake sediments.
   1. The rate of organic matter accumulation plays a major role in controlling immobilization in lake sediments.
E. What are the factors controlling the stability of lake ecosystems against changes induced by atmospheric deposition, especially acid precipitation?
   1. Groundwater flow is a major factor in the buffering capacity of the lakes of the Northern Highlands.
   2. The sensitivity and response of lakes of different typologies (dystrophic, oligotrophic, mesotrophic, and eutrophic) can be predicted by the characteristics of the watershed, i.e. forest cover and logging and burning history, amount of highland drainage, road and housing development.
   3. The sensitivity of lakes to atmospheric deposition is best predicted by lake characteristics and namely its water chemistry, surface area, and volume.
   4. Time lags in responses of lake chemistry and biota to acid deposition are in the range of decades rather than years.
F. How does the species composition and trophic structure of lakes change following the introduction of an exotic crayfish?
   1. <u>Orconectes</u> <u>rusticus</u> will dramatically alter the structure of the macrophyte, fish, and benthic invertebrate communities by consumption.
   2. These changes will alter significantly the biotic structure of the littoral zone, the pathways of carbon flow, and biogeochemical cycling.

Appendix 3. Interactions of North Temperate Lakes LTER Program with other projects

I. Interactions with short-term projects at Trout Lake.

A. Investigators at the University of Wisconsin-Madison

1. Mike Adams and Harry Boston, Botany Dept. Significance of C.A.M. and Sedimentary Dissolved Inorganic Carbon in the Photosynthetic Economy of Selected North American Isoltids. (NSF-BSR8212340)
2. Dan Schneider and Tom Frost, Center for Limnology. Responses to Disturbance in Temporary Ponds: A Test of the Influence of Successional Time on the Development of Biotic Interactions.
3. Clarence Clay, John Magnuson, Richard Nash, Timothy Stanton, Mike Jech and Paul Jacobson, Marine Studies Center. Acoustic Techniques for the Study of Nekton and Zooplankton at Water Type Boundaries and Oceanic Fronts. (ONR)
4. Thomas Frost, Center for Limnology. Alga-Invertebrate Symbioses in Freshwater Sponges. (NSF-BSR8315096)
5. Weerawan Chulakasem, Jay Nelson, John Magnuson, and Marion Meyer, Zoology Dept. Physiological and Biochemical Adaptations of Fish Reproduction and Development in Dilute, Acidic Environments.
6. Tom Brock, Bacteriology Dept. Planktonic Bacteria; Physiological and Ecosystem Ecology. (NSF-DAB-8212459)
7. Luis Marin, Tim Kratz and Carl Bowser, Geology Dept. Groundwater Hydrology and Geochemistry of Crystal Bog and Surrounding Wetland.
8. Carl Einberger, Water Chemistry Program. Quantifying Ground-water Flux to Crystal Lake.
9. John Lyons, Zoology Department. Slimy Sculpin Morphology/Biogeography.
10. Nancy Raffetto and Jeffrey Baylis, Zoology Dept. Reproductive Ecology of Small Mouth Bass in a Northern Lake.
11. Jim Hurley and Dave Armstrong, Water Chemistry Program. Transformations of n-Alkanes and Carotenoids in Recent Sediments.
12. Deb Swackhamer, Water Chemistry Program. PCB's in Remote Wisconsin Lakes.
13. Jon Manchester, Water Chemistry Program. Atmospheric Transport of PCB's.
14. Paul Doskey, Water Chemistry Program. Transformations of n-Alkanes in Crystal Lake. Also has two proposals to NSF using sediments of 2 LTER lakes.
15. Goodwin, Steven, Bacteriology Dept. Bacterial Activity in a Small Acid Lake.
16. Susan Knight, Botany Dept. Genetic Structure and Potential for Evolution in Aquatic Macrophytes.
17. Jim Kitchell, Center for Limnology, Steve Carpenter (University of Notre Dame) and James Hodgson (St. Norbert College). Cascading Trophic Interactions in Lake Ecosystems. (NSF-BSR8308918)
18. Al Swain, Center for Climatic Research. Evaluation of Lake Paleoclimate Records Using Fossil Pollen and Preserved Carbon.
19. Al Swain, Center for Climatic Research. Effects of Forest Disturbance on Trophic Status of Northern Wisconsin Lakes.

B. Other investigators

1. Malcolm Butler, University of North Dakota. Insects from North Temperate Lake Profundal Communities. (NSF-BSR8308418)
2. David Lodge (Notre Dame), Roy Stein (Ohio State), Kenneth Brown (Purdue University) and Allan Covich (University of Oklahoma). Selective Predation, Herbivory and Habitat Structure: Multiple Predators and their Impact on Freshwater Snail Communities. (NSF-BSR8500775)
3. Ruth Williams, University of Wisconsin-Milwaukee. Long Term Changes in the Distribution of Freshwater Sponge Species.

4. Craig Smith, Hobart and William Smith Colleges. Analyses of Birge and Juday Phytoplankton Data.
5. Wisconsin DNR - Research, TeTra-Tech Inc. Application of ILWAS Model to Crystal Lake. In cooperation with Carl Bowser, Mary Anderson and Galen Kenoyer.
6. Argonne National Labs, Brookhaven National Labs, Oak Ridge National Lab, Battelle N.W., Dept. of Energy. Experimental Manipulations of Forest Area (proposed).
7. Walter Whitford, Walt Conley, Jim McKay (New Mexico State University), Thomas Frost and Carl Bowser. Biological and Chemical Studies of a Temporary Playa at Jornada LTER Site.
8. Snopek, Mark, Center for Great Lake Studies, University of Wisconsin-Milwaukee. Bacterial Production in Dystrophic Lakes.
9. John Titus, SUNY-Binghamton. Macrophyte Dynamics in Acid Sensitive Lakes. (S.R. Carpenter and J.E. Titus. 1984. Composition and spatial heterogeneity of submersed vegetation in a softwater lake in Wisconsin. Vegetio. 57:153-165).
10. Herbert Dutton, Hormel Institute, Minnesota. Production and Respiration of Algal Symbionts within Freshwater Sponges.
11. Interaction with Blair F. Jones (U.S.G.S., Reston), Dennis Wentz (U.S.G.S., Madison), Carl Bowser, and David Krabbenhoft. Evidence for Road Salt Effects on Local Groundwater.
12. Niwot Ridge LTER Site: Inquiry on future colaborative resesarch on lake biogeochemistry.

II. Interactions with long-term projects

<u>A. Investigators at the University of Wisconsin-Madison</u>

1. John J. Magnuson (Center for Limnology), David Le Cren and Charlotte Kipling (Windemere Laboratory of the Freshwater Biological Association of the United Kingdom), Grandville Tunnicliffe-Wilson (Department of Mathematics, University of Lancaster, UK) and Steve Serns (Wisconsin Department of Natural Resources). Long Term Patterns in the Growth of Fishes in Lake Windermere, England and Escanaba Lake, Wisconsin.
2. Tom Frost, John Magnuson, and Tim Kratz, Center for Limnology. Analyses of the Effects of Increased Acidity on Lake Ecosystems by a Whole Lake Manipulation Experiment: Site General Activities and Zooplankton Studies. (EPA-CR810941-01-0)
3. Mike Adams, Botany Department. Program on Lake Maggiore, Italy in conjunction with Italian scientists.

<u>B. Other investigators</u>

1. Steve Serns, Wisconsin Department of Natural Resources. Five Lakes Experimental Fisheries Project.
2. National Atmospheric Deposition Program. Rainfall and Chemical Composition.
3. Pat Brezonik and James Perry, University of Minnesota. Responses of Little Rock Lake to Artificial Acidification: Water Chemistry, Productivity, Nutrient Cycling and Hydrology Phases. (EPA-CR810981-01)
4. Pat Brezonik, University of Minnesota. Hydrogen Ion Neutralization by Bacterial Sulfate Reduction. (EPA-CR811540-01)
5. Paul Garrison and Kathy Webster, Wisconsin Department of Natural Resources. Acid Rain: Aquatic Effects - Little Rock Lake (EPA-CR810961-01-02).
6. Bill Swenson, University of Wisconsin-Superior. Fish Population Changes and the Mechanism Associated with Change in an Acidified Lake: Pre-Acidification

Period. (EPA-CR810934-01-3).

7. William Rose, U.S.G.S. Hydrology of Little Rock Lake.
8. Lee Adrias (Cooperative Weather Station, Rainbow Flowage) and Terry Strong (Department of Agriculture, Harshaw). Solar Radiation Data Collection - 1977 to present.

III. Requests for use of LTER data

A. <u>Investigators at the University of Wisconsin-Madison</u>

1. Graduate Students:
   Paul Jacobson - Crystal Lake gill net data
   Harry Boston - Water chemistry of Firefly Lake
   Harry Boston - Water chemistry of Crystal Lake
2. Limnology class requests:
   Lake Mendota fish data, chlorophyll, secchi disk, phosphorus concentrations
3. Senior Thesis:
   John Osborne, 1982-83. Chemical and physical data for bog 27-2

B. <u>Other investigators</u>

1. Art Ensign, Wisconsin DNR-North Central District Headquarters: Description of fish database and examples of standard tables generated from the database.
2. Steve Serns, Wisconsin DNR: Changes in cisco and smelt abundance in Sparkling Lake; changes in cisco and walleye in Big Musky Lake.
3. Dr. Ellie Prepas, Dept. of Zoology, Biological Sciences Centre, University of Alberta, Edmonton, Alberta, Canada: Lake Mendota 1979-81 data on the vertical distribution of nitrogen (inorganic and total) and phosphorous (total and dissolved).
4. Dr. Walter Rast, Research Hydrologist, Geological Survey, U.S. Dept. of Interior: nutrients, carbon, major cations and anions, chlorophyll levels, water transparency, alkalinity, pH and physical data.
5. Gmur, US-EPA: Chemical data on Wisconsin lakes in respect to cultural acidification.

IV. Visiting scientists

1. Liao Guozhang, People's Republic of China. Variability among Years and Lakes in Littoral Zone Fish Assemblages in Six Wisconsin Lakes. With John Magnuson.
2. Maura Gage, Palomar College, California. Vegetation of the Watershed of the Northern Lakes LTER Program.

Appendix 4. Table 1. Sites for Meterological Data Collection within 50 km of the Trout Lake Station with the Dates and Types of Data.

HISTORICAL METEOROLOGICAL DATA

Location	Distance to T.L. Station	Period of Collection	Data On UW Computer	Types of Data
Five Lakes Research Site Escanaba Lake Steve Searns 715-356-5212	8.5km	1958 - Present		Max/Min Temp. Open Water Surface Temp.
Harshaw-North Central Forest Exp. Station Terry Strong 715-362-7474 (USFS)	38.6km	1977 - present		Total Solar Rad. ('81)
Minocqua ($) (WVIC)	11.0km	1903 - Present	* 1905 - 1981 ** 1931 - 1981	Max/Min Temp. PPT. Pre.Wind(03-48)
National Atmos. Deposition Prog. Site (NADP) Trout Lake Mark Johnson	4.1km	1980 - Present		PPT. Dry Deposition (Amount and Total Chemistry)
Rainbow Flowage($) Dam Lee Adrias 715-277-2430 (WVIC)	22.5km	1944 - Present	* 1948 - 1981 ** 1948 - 1981	Max/Min Temp. PPT. Wind (Length)('46) Evap.('46) Hum.Bar.Press.(46-51) Snow on Ground('74)
Rest Lake Dam($) Galvin Laporte (Private Indiv.)	21.4km	1913 - Present	* 1949 - 1981 ** 1931 - 1981	Max/Min Temp. PPT. Prev.Wind(13-48) Snow on Ground('18)
Rhinelander($) Airport (F.A.A)	48.3km	1908 - Present	* 1948 - 1981 ** 1931 - 1981	Max/Min Temp. PPT. Pre.Wind(08-48) Snow on Ground(08-48)
St.Germain Dam($) 715-345-4163 (WVIC)	15.0km	1910 - Present	* 1931 - 1981 ** 1931 - 1981	Max/Min Temp. PPT. Pre.Wind(10-49) Snow on Ground(10-74)
Trout Lake (UW LTER Program)		1982 - Present		Max/Min Temp. PPT.(82) Hum.('82)

* Daily Data $ Cooperative Weather Station
** Monthly Averages @ Synoptic Weather Station
WVIC Wis. Valley Improvement Corp. (Supplementary)
---- Monthly Summaries are available from the State Climatologist for beginning to 1932 and 1951 to 1981.

Appendix 5. The Little Rock Lake Experimental Acidification Study.

The Little Rock Acid Rain Research Project is a long-term multidisciplinary study being conducted by the University of Wisconsin-Madison, University of Wisconsin-Superior, University of Minnesota, University of Minnesota-Duluth, the U.S. Geological Survey, the U.S. Environmental Protection Agency (USEPA), and the Wisconsin Department of Natural Resources. It is funded through the U.S. Environmental Protection Agency. The project is designed to show the effects of acid rain on a softwater lake system by intentionally adding acid to half the lake and observing resultant changes in water chemistry, fish populations, plants and other aquatic life.

The study design consists of a 2-year pre-acidification period during which baseline biological conditions and variability will be observed. In-situ (e.g. limnocorral) and laboratory experiments will be conducted during the second year to help refine hypotheses and analysis techniques, and to define the rate and duration of acidification. Acidification will begin in the third year and is expected to take approximately 4 or 5 years to complete. The study lake was selected largely because it contains 2 very similar basins connected by a narrow channel. These have been separated by a removable barrier. One side will be acidified, the other will serve as a reference. The lake contains six fish species including bass, walleyes, yellow perch, and minnows.

The major objectives of the Little Rock Lake study are: 1) to determine the responses to artificial acidification of a low alkalinity, warm water fish dominated lake; 2) to determine and compare the significance of direct (water chemistry mediated) and indirect (food chain mediated) effects of acidity on organisms in the lake; 3) to determine the mechanisms of response of ecosystem components through detailed chemical and biological observation, in-situ experimentation, and directly related laboratory testing; 4) to relate the observed effects on Little Rock Lake to the sensitivity and potential for acid precipitation impacts of other lakes; and 5) to determine the degree of generality of acid rain biological effects on lake in different geographic areas (Canadian Shield, Adirondak Mountains, northern Florida, upper Midwest, etc.).