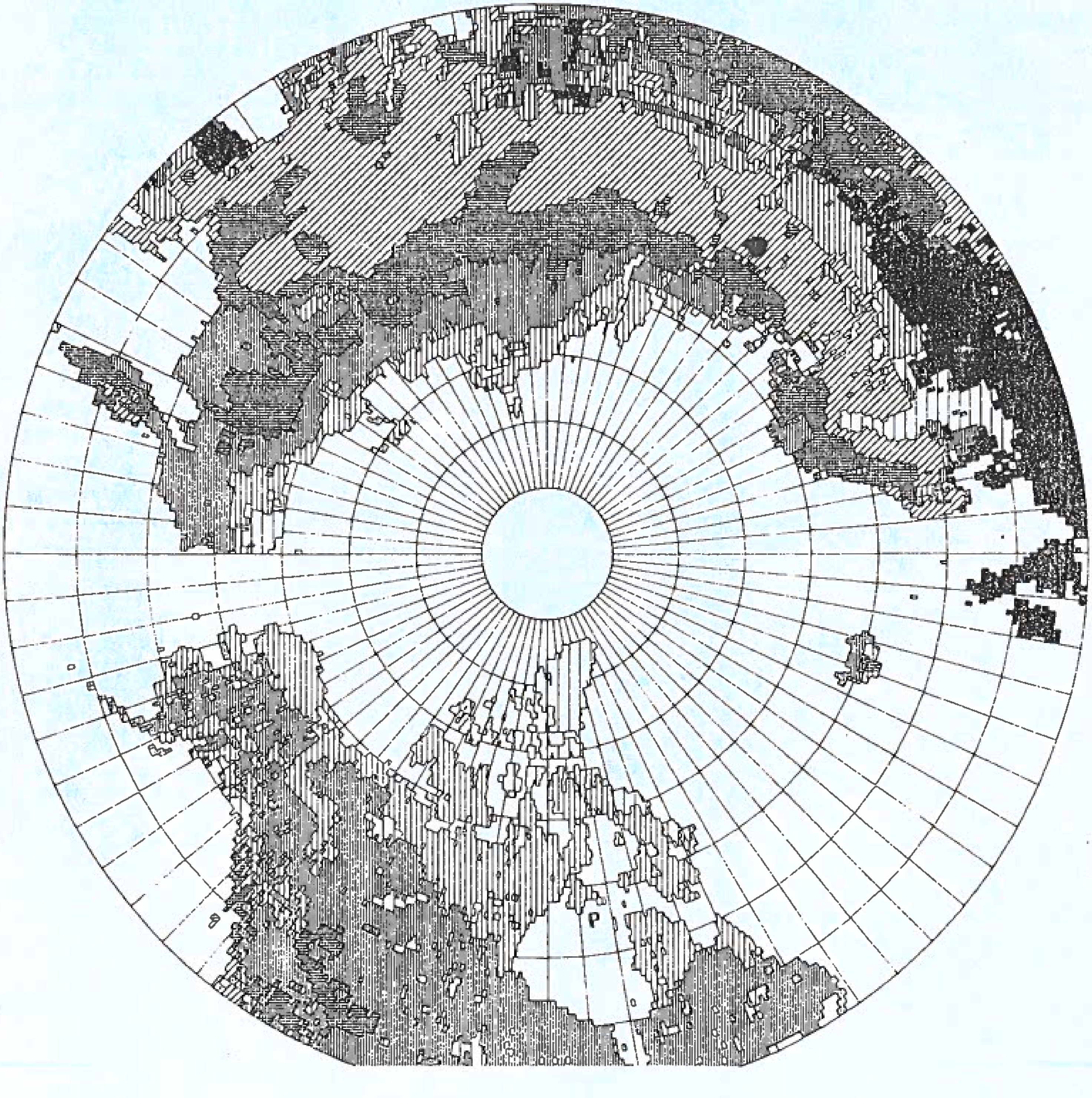
Arctic LTER
Site Review

Toolik Lake 12-13 July 1991



The Arctic LTER Project

A Terrestrial and Freshwater Program for Regional Change

Investigators

John E. Hobbie
The Ecosystems Center, Marine Biological Laboratory
W. John O'Brien
Department of Systematics and Ecology, University of Kansas
Bruce J. Peterson
The Ecosystems Center, Marine Biological Laboratory
Gaius Shaver
The Ecosystems Center, Marine Biological Laboratory
Linda A. Deegan
The Ecosystems Center, Marine Biological Laboratory
Brian Fry
The Ecosystems Center, Marine Biological Laboratory
Anne E. Giblin
The Ecosystems Center, Marine Biological Laboratory
Anne E. Hershey
Department of Biological Sciences, University of Minnesota-Duluth
George W. Kipphut
Center for Great Lakes Studies, University of Wisconsin
Arthur E. Linkins
Clarkson University, Potsdam, New York
Michael E. McDonald
Department of Civil Engineering, University of Minnesota, Duluth
Michael C. Miller
Department of Biological Sciences, University of Cincinnati
Knute J. Nadelhoffer
The Ecosystems Center, Marine Biological Laboratory
Edward B. Rastetter
The Ecosystems Center, Marine Biological Laboratory

TABLE OF CONTENTS

ABSTRACT

A research project at Toolik Lake, located in the northern foothills of the Brooks Range, Alaska, has collected data since 1975 from tundra, lakes, and streams and in 1987 became a part of the U.S. Long Term Ecological Research Program (LTER). The broad goal of the project is to understand and predict how these arctic ecosystems function and how they respond to change. A specific goal is to understand the extent of control by resources (bottom-up control) or by grazing and predation (top-down control) and to understand the exchange of nutrients between land and water.

A part of the project is to monitor year-to-year variability and to measure long-term changes. In lakes this includes measurements of temperature, chlorophyll, and primary productivity, in streams this includes weather, nutrients, chlorophyll, insects and fish and on the tundra this includes flowering, air temperature, solar radiation, and biomass.

The heart of the LTER project is the long-term experimental manipulations of ecosystems to examine processes and the effects of change. These include the fertilization of lakes and streams, the addition and removal of lake trout from lakes, and the shading, fertilizing, and heating of the tussock tundra.

The data collected in plots on the tundra and in small areas of the stream and lakes will be scaled up to the whole watershed level through mathematical modeling. In the future, the watershed model will be interactive with geographically located data bases so the model and process information may be extrapolated to the larger region. A prediction may then be made for such questions as the future export of nutrients from the whole of the North Slope of Alaska when temperature and precipitation changes.

INTRODUCTION

Why an Arctic LTER Site?

Basic ecology. Arctic tundra represents a major biome and must be studied as a part of the biosphere. Some of the fundamental questions of ecology, such as the extent of control of herbivore population structure by predation, are best studied in the Arctic where species diversity is low.

Comparative ecology. Processes and their controls must be investigated at the extreme ends of the climatic spectrum, and if comparative ecological analysis within the LTER network is to work then the arctic data must be a part.

Applied science. Northern Alaska is developing rapidly and research can answer several applied questions such as how to minimize the impact of development on ecosystems and what will be the effect of fishing on unexploited lakes. There are also the series of questions about the Arctic's response to global change. According to General Circulation Model scenarios, there will likely be a strong temperature increase during the winter in the Arctic (>6°C) so arctic systems need to be monitored for early signs of change.

Description of Site

Field research of the Arctic LTER is based at Toolik Lake, Alaska, in the northern foothills of the Brooks Range (68°38'N, 149°43'W, elevation 760 m) (Fig. 1). The actual LTER designated site consists of the two watersheds that make up the entire upper reaches of the Kuparuk River. The western watershed includes Toolik Lake; the eastern watershed is called the upper Kuparuk River. Tussock tundra is the dominant vegetation form but there are extensive areas of drier heath tundra on ridge tops and other well-drained sites as well as areas of river-bottom willow communities.

The climate of Toolik Lake is typical of arctic regions, with a mean annual air temperature of about -7°C and low precipitation (50% of the 20-40 cm of precipitation falls as snow). The sun is continuously above the horizon from mid-May to late July. The snow-free season lasts from late May to mid-September, with below-freezing temperatures possible at any time. The entire region is underlain by continuous permafrost which exerts a major influence on the distribution, structure, and function of both terrestrial and aquatic ecosystems.

The primary focus of the streams research is the Kuparuk River, a fourth-order stream where it crosses the Dalton Highway about 10 km northeast of Toolik Lake. The watershed above the road crossing is 143 km^2. The river is oligotrophic and contains but one species of fish, the arctic grayling. Flow commences with spring runoff in early- to mid-May and ends in mid- to late-September when the river riffles dry up completely and the pools freeze completely. Many of the other streams that cross the highway have also been surveyed and compared.

Toolik Lake (= Loon Lake) has a surface area of 150 ha and a maximum depth of 25 m. The ice thickness reaches 1.5 m and lasts from early October until mid June. The lake stratifies in the summer and surface temperatures may reach 18°C during warm summers. Because of the low input of nutrients in the streams, the lake is oligotrophic with a primary productivity of around 12 g C m^2 yr^{-1}. Lake trout, sculpin, and grayling are the dominant fish.

Goals of the Arctic LTER Project

To understand how tundra, streams and lakes function in the Arctic and to predict how they respond to changes including climate change.

The ecosystems of the foothills of the North Slope of Alaska are not in an equilibrium state but are changing in response to exploitation of the native populations of top predator fishes and other animals and perhaps even in response to a warming climate in the Arctic. Other changes due to development of energy resources and global climate change are likely. Predictions of ecological change based upon understanding of the function of terrestrial and freshwater ecosystems are needed.

To reach this objective the project will:

Determine year-to-year ecological variability in these systems and measure long-term changes.

Understand the extent of control by resources (bottom-up control) or by grazing and predation (top-down control).

Measure rates and understand the controls of the exchange of nutrients between land and water.

Research efforts in the five LTER core areas

To encourage the comparative approach to ecological studies, all LTER sites are required to include research efforts in five core areas. These areas are listed in some detail in Table 1 and may be briefly summarized as primary production, populations representing trophic structure, organic matter accumulation, nutrients and their movements, and disturbance.

The Arctic LTER project makes measurements in all of these areas and uses disturbance, both natural and artificial, as a tool for creating experiments. A number of specific examples of how the Arctic LTER research fits into these categories are given in Table 1. It will be noted that the fit is not perfect; for example, streams do not accumulate organic matter and we have no studies of trophic structure in the terrestrial ecosystems. This does not mean that there have been no measurements of animals and their activities on land because other, non-LTER scientists have made measurements (see Appendix III for listing of published and accepted manuscripts from the Toolik site; some of these, such as Batzli and Henttonen (1990) on microtines, address higher animals). Other studies have been made of reindeer feeding in tundra by R. White of the University of Alaska so the topic has been addressed.

History of Research: Present-day Experimental Approach

The Arctic Research Laboratory, funded by ONR and centered at Barrow, supported research on the North Slope from the late 1940's until the late 1970's. Lakes, ponds, and terrestrial vegetation were described in surveys and a few detailed studies throughout the region. Between 1971 and 1974 the International Biological Program (IBP, NSF) carried out detailed seasonal and process studies on coastal tundra, ponds, and lakes at Barrow with some additional research at Prudhoe Bay. Three book-length synthesis volumes were produced. A follow-up limnological study moved to Toolik Lake in 1975 to provide information on foothill lakes, previously virtually unknown. The opening of the pipeline road in 1976 and the presence of the field camp soon attracted terrestrial scientists to study the tussock tundra of the region, which is very different from the coastal tundra. A series of NSF and DOE projects at Toolik Lake have now provided information comparable to the Barrow data set.

Ecological research in the Toolik region was mainly observational for the first five years; now it is mainly experimental with the focus on the effects of manipulating whole systems. The list of manipulations that have been carried out in the vicinity of Toolik Lake is given in Table 2. Arctic ecosystems with their low canopies, strong nutrient limitation, and low number of species, are particularly easy to manipulate and the approach has been very successful.

Terrestrial research in the Toolik area began in 1976 with descriptive and baseline vegetation studies of many sites along the length of the Dalton Highway and at Toolik Lake. The next phase, research on the response of plants to disturbances of pipeline and road construction, led to studies of plant demography and population dynamics and raised questions of controls on long-term successional patterns and the regulation of plant growth form and composition of the vegetation. From 1979 to 1982, plant growth and its controls were analyzed and a number of long-term experiments (fertilization, light, temperature) were set up. The principal conclusion, that soil processes and nutrient availability were more important than light and temperature in limiting annual productivity, led in 1985 to an NSF-Ecosystem project on element cycling in the tundra landscape.

The aim of the "landscapes" project was to evaluate the importance of lateral N and P fluxes in soil water moving downslope across the surface of the permafrost. To do this we have had to develop and compare overall N and P budgets for the various ecosystems through which the water flows, and to link these budgets with a hydrologic model.

Intensive research on the Kuparuk River began in 1978, and its water chemistry, flow, and major species populations have been monitored for over 10 years. For much of this time, a section of the river has been fertilized by the continuous addition of fertilizer. Recently, the abundance of the single species of fish in the river, the arctic grayling, was manipulated in various sections of the river to examine the effects of predation. In 1989, a monitoring program was begun in Oksrukuyik Creek, a slightly smaller third-order stream about 15 km to the northeast, with the intention of developing a long-term comparison with the Kuparuk River.

Intensive research on Toolik Lake began in 1975 with surveys of the biota, chemistry, and processes ranging from primary productivity to nutrient budgets. In the 1980's the research was concentrated on the question of controls of populations, community structure, and processes. Large (60 m^3) plastic bags were set up for manipulations of nutrients and predators. Several whole lakes and parts of lakes have received similar nutrient and predator treatments. In the surrounding glacial moraine there are dozens of lakes ranging from small thaw ponds to lakes more than 1 km wide and 20 m or more in depth. These lakes were surveyed extensively in the mid-1970's and compared in terms of their chemistry, productivity, species composition, and trophic structure. More recently the survey work has been extended to parts of the Arctic coastal plain and Brooks Range, as well as the northern foothills region.

Management of the LTER Project

Hobbie is the overall director while Shaver, Peterson, and O'Brien direct the tundra, streams, and lakes sections, respectively. Meetings of all the scientists are held at Toolik Lake during early July when most are in camp and an annual meeting is held at a central location in February or March.

The general philosophy of management is collegial with major decisions, such as the experiments to be carried out, being made by the entire group. The executive group of four make the day-to-day decisions. The large experiments are maintained and basic monitoring is carried out by technicians under LTER funding. Individual scientists and their students are responsible for other measurements of the results of the experiments. There is also the opportunity for individual scientists to carry out other related research along their own lines of interest.

Long-term monitoring and data sets

The LTER program has taken the responsibity for the long-term monitoring of key environmental and biological variables. This monitoring includes climatic parameters, lake and stream chemistry, and annual variation in growth and reproduction of key terrestrial and aquatic populations. A list of the monitored variables is given in Table 3.

To keep track of the LTER data, the Arctic LTER maintains at the Marine Biological Laboratory a computerized data base which contains a wide variety of long-term data sets. These data sets, such as 10 years of flow data for the Kuparuk River, are available to other researchers. Detailed information on the procedures and formats followed are given in Appendix I.

Education

Research leading up to the LTER and since 1988 has supported the research of many graduate and undergraduate students. Projects at the Toolik site have produced 10 Ph.D. and 16 Master's theses (see Appendix III). Our efforts in undergraduate education have expanded with the REU program of NSF, and in 1991 we have two REU's in residence at Toolik.

The Toolik Lake Research Camp

This facility is owned and operated by the University of Alaska; the daily fee ($112 in 1990 and 1991) covers room, board, and camp use. Facilities include 5 heated and electrically-powered laboratory trailers, a large kitchen/dining/common area with general-use computers and communications facilities, several dormitory trailers, and shop, storage, and wash-up trailers. Stable power is supplied by a generator. General-use scientific equipment includes drying ovens, balances, a deionized water system, and three small boats. Additional equipment and vehicles must be provided by the research teams.

The camp capacity is 40 scientists. During the summer months (May through September) there are 4 staff members in camp, with an additional 2 logistic support personnel in Fairbanks. One trailer is available for short-term winter visits.

Relationship to Other Projects at Toolik Lake

The Toolik Lake LTER research is closely integrated with two separately-funded research programs also based at Toolik Lake, and collaborates to vari-

Table 1. The five research areas common to LTER sites and the corresponding measurements being carried out at the Arctic LTER site.

---

(1) Primary production, pattern and control

Tundra: biomass production control by nutrients, light, temperature; exclosures to test effects of herbivores; annual and regional variation

Streams: production control by nutrients, grazers; natural variations, seasonal, yearly, and between streams

Lakes: primary production natural variation measured seasonally, yearly, and between lakes; control of production by nutrients, grazers

(2) Populations representing trophic structure, spatial and temporal distribution

Streams: algae (chlorophyll), insects, fish; ^{15}N gives trophic level, ^{13}C gives food resources; isotope comparisons with other LTER's

Lakes: phytoplankton and benthic algae (species, chlorophyll); zooplankton, insects, molluscs, fish; ^{15}N distribution gives trophic level, ^{13}C gives food resources; isotope comparisons with other LTER's

(3) Organic matter accumulation in soils and sediments, pattern and control

Tundra: long term accumulation by ^{14}C dating; decomposition in lab and field; comparative decomposition with other LTER's; effects of fertilizer and greenhouse treatments

Lakes: sediment accumulation by ^{14}C; sediment trap studies; benthic respiration in chambers; nutrient addition effects on sedimentation and respiration; controls of sulfur accumulation, sediment cores

(4) Nutrients, inorganic inputs and movement through soils, groundwater, and surface waters

Tundra: nutrient budgets of contrasting ecosystems; water and nutrient transport between systems on a toposequence; exchange of gases between tundra and atmosphere; export of nutrients and dissolved organic matter from experimental watershed

Streams and Lakes: output budget for Kuparuk River and for Toolik feeder stream; input budget for Toolik Lake; seasonal and yearly variations in nutrients; nutrient transformations in riparian and hyporheic zone; flux of CO_2 and CH_4 from surface waters to atmosphere; ^{18}O distributions in snow, springs, surface water

(5) Disturbance at site, pattern and frequency

Tundra: measurement of long-term change of communities due to climate change; amount of disturbance by road dust; population dynamics of native and exotic plant species; short and long term effects of nutrient addition

Streams: chemical and biotic response to eutrophication; measurement of fishing pressure and effects of removal of fish on trophic structure; extreme natural variations in snowmelt, discharge

Lakes: chemical and biotic response to eutrophication; disturbance of trophic structure caused by removal of top predator, the lake trout; variations in primary production caused by natural changes in discharge and resulting changes in nutrient input

---

Table 2. Whole system experimental manipulations in tundra, streams, and lakes at Arctic LTER site.

Terrestrial		
Factorial NPK fertilizer treatment - Toolik, Sag		1976-, 1986-present
Factorial greenhouse, shade, fertilizer		1979-1982, 1980-present
Herbivore exclosures		1989-present
Soil warming		1991
Kuparuk River		
P addition	added at 0.59 Km below control	1983-1990
N+P addition	added at 2 Km below control	1986, 1989
Grayling density	grayling, control/fert	1985-present
^{15}N addition	add $^{15}NH_4Cl$-weekly samples	1991
Oksrukuyik Creek		
P addition	2 Km upstream from Haul Road	begin 1991
Black fly removal	near Sag. confluence	baseline 1991, begin 1992
Grayling density	grayling, control/fert	1990-present
Toolik Lake		
Limnocorrals - N, P, N+P, fish	6 corrals in lake	1983-1986
Limnocorrals - NH_4 vs NO_3 uptake	2 corrals in lake	1988-1989
DOC addition, bacteria	small limnocorrals	1991
Exclosure cages	snails	1990
Lake N-2 Divided lake		
N+P addition	fert side	1985-1990
^{15}N addition to lake	fert and control side	1988
Exclosure cages	snails	1990
Lake N-1 N+P addition	lake trout present	1990-present
Lake I-8 Lake trout	slow removal	1989-present
Lake NE-12 Lake trout	fast removal	1988-present
Lake S-6 Lake trout	introduction	1988-present
Lake E-1 Sculpin	introduction	start 1991
Lake N-3 Sculpin	removal	start 1991

Table 3. Summary of the Arctic LTER Long-Term Monitoring Program.

	LOCATION	FREQUENCY	DURATION OF COLLECTION
KUPARUK RIVER			
DISCHARGE	AT ROAD	CONTINUOUS/SUMMER	1983-1990
NUTRIENTS	11 STATIONS	WEEKLY/SUMMER	1983-1990
PHYSICS AND CHEMISTRY: (pH, ALKALINITY, TEMPERATURE, CONDUCTIVITY, CATIONS AND ANIONS)	11 STATIONS	WEEKLY	1983-1990
CHLOROPHYLL: (SESTONIC AND EPILITHIC)	11 STATIONS	4X/SUMMER	1983-1990
FISH GROWTH, (LENGTH AND WEIGHT)	CONTROL/FERT	2X/SUMMER	1985-1990
INSECTS	8 STATIONS	3X/SUMMER	1988-1990
ISOTOPES	10 STATIONS	4X/SUMMER	1988
OKSRUKUYIK RIVER			
DISCHARGE	AT ROAD	CONTINUOUS/SUMMER	1988-1990
NUTRIENTS	9 STATIONS	WEEKLY/SUMMER	1989-1990
PHYSICS AND CHEMISTRY: (pH, ALKALINITY, TEMPERATURE, CONDUCTIVITY, CATIONS, ANIONS)	9 STATIONS	WEEKLY/SUMMER	1989-1990
CHLOROPHYLL: (SESTONIC AND EPILITHIC)	9 STATIONS	4X/SUMMER	1989-1990
FISH GROWTH, (LENGTH AND WEIGHT)	2 STATIONS	2X/SUMMER	1989-1990
INSECTS	8 STATIONS	4X/SUMMER	1989-1990
ISOTOPES	8 STATIONS	4X/SUMMER	1989-1990
TOOLIK LAKE			
PHYSICS AND CHEMISTRY: (OXYGEN, TEMPERATURE, CONDUCTIVITY, pH, ALKALINITY, LIGHT, SECCHI DEPTH, CATIONS, ANIONS)	EVERY METER	WEEKLY/SUMMER	1975-81, 1983-1990
NUTRIENTS	0,1,3,5,8,12,16M	WEEKLY	1975-1981, 1983-1990
SESTONIC CHLOROPHYLL	0,1,3,5,8,12,16M	WEEKLY	1975-1981, 1983-1990
PRIMARY PRODUCTION	0,1,3,5,8,12,16M	WEEKLY	1975-1981, 1983-1990
ZOOPLANKTON	0-10 METERS	WEEKLY	1975-1990
INSECTS	BENTHOS	YEARLY	1988-1990
FISH GROWTH, (LENGTH AND WEIGHT)	WHOLE LAKE	YEARLY	1986-1989
TOOLIK INLET DISCHARGE	200 M FROM LAKE	CONTINUOUSLY	BEGIN 1991
ISOTOPES	CENTER STATION	4X/SUMMER	1987-1989
POM	SURFACE		
ZOOPLANKTON	0-10 METERS		

LAKE N-2 (Table 3 cont.)

	LOCATION	FREQUENCY	DURATION OF COLLECTION
PHYSICS AND CHEMISTRY: (OXYGEN, TEMPERATURE, CONDUCTIVITY, pH, ALKALINITY, LIGHT, SECCHI DEPTH, CATIONS, ANIONS)	0,1,3,5,7 METERS	WEEKLY	1986-1990
NUTRIENTS	0,1,3,5,7 METERS	WEEKLY	1986-1990
SESTONIC CHLOROPHYLL	0,1,3,5,7 METERS	WEEKLY	1986-1990
PRIMARY PRODUCTION	0,1,3,5,7 METERS	WEEKLY	1986, 1988-1990
ZOOPLANKTON	5 M VERT. TOW	WEEKLY	1983-1990
INSECTS	BENTHOS	3X/SUMMER	1988-1990
FISH GROWTH, (LENGTH AND WEIGHT)	WHOLE LAKE	YEARLY	1985-1990
ISOTOPES	CONTROL SIDE	4X/SUMMER	1987-1989
POM	SURFACE		
ZOOPLANKTON	0-5 M		

LAKE I-8

PHYSICS AND CHEMISTRY: (OXYGEN, TEMPERATURE, CONDUCTIVITY, pH, ALKALINITY, LIGHT, SECCHI DEPTH, CATIONS, ANIONS)	0,1,3,5,8,12 M	3X/SUMMER	1986, 1989-1990
NUTRIENTS	0,1,3,5,8,12 M	3X/SUMMER	1986, 1989-1990
SESTONIC CHLOROPHYLL	0,1,3,5,8,12 M	3X/SUMMER	1986, 1989-1990
PRIMARY PRODUCTION	0,1,3,5,8,12 M	3X/SUMMER	1986, 1989-1990
ZOOPLANKTON	0-10 METERS	3X/SUMMER	1986, 1989-1990
INSECTS	BENTHOS	3X/SUMMER	1986, 1989-1990
FISH GROWTH, (LENGTH AND WEIGHT)	WHOLE LAKE	YEARLY	1986, 1989, 1990

TERRESTRIAL: MESIC TUSSOCK TUNDRA, HEATH, WET SEDGE, SALIX SHRUB SITES

FLOWERING DATA	HAUL ROAD TRANSECT,	YEARLY	1977-1990
NITROGEN MINERALIZATION			1986-1990
WEIGHT PER TILLER	*Eriophorum vaginatum*		1977-1990
PLANT BIOMASS			1985, 1988, 1989
RAIN CHEMISTRY	pH, NUTRIENTS	WEEKLY	1988-1990

WEATHER STATIONS:

TOOLIK LAKE, TOOLIK MESIC TUSSOCK TUNDRA, KUPARUK CROSSING, KUPARUK HEADWATERS, SAGAVANIRKTOK RIVER HEATH

AIR TEMPERATURE	MAX, MIN AND AVERAGE	1988-1990
WIND	SPEED, DIRECTION	1988-1990
RELATIVE HUMIDITY		1988-1990
PRECIPITATION		1988-1990
INSOLATION	PHOTOSYNTHETICALLY ACTIVE RADIATION (PAR)	1988-1990
NET RADIATION		1988-1990
SOLAR RADIATION		1988-1990
SOIL TEMPERATURE	DIFFERENT DEPTHS	1988-1990
BAROMETRIC PRESSURE		1990
TOOLIK LAKE TEMP.		1988-1990
TOOLIK LAKE DEPTH		1988-1990
KUPARUK RIVER LEVEL		1988-1990

ous degrees with several others. This integration and collaboration includes the joint design, maintenance, and sampling of large, long-term experiments, the sharing of data, equipment, laboratories, and personnel, and the writing of books and scientific papers.

<u>DPP Project on Freshwater Processes</u>: A current project on streams and lakes, funded by NSF's Division of Polar Programs, was refunded for 3 years beginning in May 1991. The goals of this project overlap with the LTER goals and it is combined with the LTER for joint administration (financially) under OPASS. The abstract from the proposal states "Continuing research is aimed at the regulation of processes and populations by resource limitation (bottom-up control) and by predation (top-down control). Nutrients will be added to rivers and to lakes and the effect of the changes followed throughout the food web. Lake trout and grayling, the top predators of lakes and streams, will be added or removed to determine the effects of top-down control on community structure. In all the research, the emphasis will be on understanding the controls of the interactions and processes; armed with this knowledge we will understand how these systems operate at present and how they will change in the future.

New stream research will test the role of black flies by removing these insects from a stream reach, test the role of invertebrate predators (a predaceous caddis fly), test the role of fish predation, and determine the stream food web with isotopes of carbon and nitrogen (natural abundance, addition experiments). New lake research will focus on measurements of the quantity and usability of the dissolved organic carbon and dissolved organic nitrogen entering Toolik Lake, investigate the effect of adding a strong planktivore (least cisco) to lakes, and test the importance of sculpin as an intermediate predator. This knowledge will be extended through surveys of other lakes on the North Slope and through modeling.

A second goal is to understand the controls of the nutrient release from land to streams and lakes as well as to understand the transformations of nutrients and carbon in these waters. We will investigate the interactions of land and water by determining the quantity of nutrients entering the river from different types of tundra vegetation and the role of the riparian zone and the upstream lakes in modifying stream chemistry."

<u>NSF-Ecosystems project on terrestrial biogeochemistry</u>: Since 1985, the "Landscapes" project has been funded by NSF-Ecosystem Studies. This group is currently seeking renewal funding. The focus of their proposed renewal is carbon and nutrient interactions in contrasting tundra ecosystem types, specifically in the context of global climate change. Their proposed research will be done in close collaboration with fertilizer, greenhouse, and shade experiments established and maintained by the LTER. The work will also include controlled-environment experiments on soils, plants, and soil-plant microcosms; these experiments are designed to be complementary to the LTER field experiments.

The original focus of this group was on quantifying element transport over the tundra landscape in soil water, and on the importance of that transport to element cycling along a toposequence of contrasting ecosystem types. Since the bottom of their toposequence ended in a stream, their work has been useful in development of our current thoughts on land-water interactions and the varying importance of different terrestrial ecosystem types in regulating element inputs to aquatic systems. This group's currently-planned research on carbon and nutrient interactions includes a strong interest in controls on carbon and element losses from terrestrial to aquatic ecosystems.

<u>EPA trace gas project</u>: For the next two years Knute Nadelhoffer and Josh Schimel, with funding from EPA, will be measuring CO_2, CH_4 and N_2O emissions from a variety of sites at both the Toolik Lake and the Bonanza Creek LTER sites. Results from our field experiments and our planned soil incubation experiments will help to explain the broader patterns they observe, and their results will help us greatly in extrapolating our results to other tundra and boreal forest sites. Bill Reeburgh and Steve Whalen are continuing their EPA-funded work on trace gases along the Alyeska oil pipeline, including Toolik Lake.

<u>Mellon Project on Arctic Modeling</u>: The Andrew W. Mellon Foundation provided partial support for a postdoctoral fellow and now research associate, George Kling, to work on the LTER project during 1990-91. Dr. Kling paid special attention to the land-water interactions part of the project and carried out measurements on the movement of CO_2 and CH_4 from soils to lakes and streams and on nutrient movement through soils. The goal of this research is to lay the groundwork for modeling of the land-water interactions.

<u>The DOE R4D Project</u>: The scientists funded by the DOE-R4D program, also based at Toolik Lake since 1984, are winding up the second phase of their research. As part of a book synthesizing their results so far, Gus Shaver has written a review chapter on the history of integrated ecosystem research in Alaska up to 1990. More importantly we have developed a plan to apply our data to a separate series of simulation models developed by the R4D group. This will provide an independent test of conclusions based on our General Ecosystem Model (GEM). Field data, produced by the R4D group, strongly support our earlier ideas about nutrient limitation and the importance of nutrient transport between landscape units, but their data and models also suggest a more important role of soil moisture in determining landscape patterns. Soil moisture and its relationship to soil oxygen availability and respiration/mineralization linkages may provide an explanation for this contrast between their results and ours.

<u>Relationship to Other LTER Projects</u>

The Toolik Lake LTER program has interacted with researchers from other LTER sites in numerous ways. These interactions have included two workshops held in Woods Hole, on decomposition processes and on the use of stable isotopes in ecosystem studies. The workshop on decomposition processes led directly to a proposal (now funded by NSF) on litter decomposition that includes about 20 sites in North and Central America. The aim of the project is to compare decomposition of standard litter types that have been distributed to all sites. A second, longer-term intersite project, on the effect of manipulation of litter inputs on long term accumulation and cycling of soil organic matter, is now in the planning stages. We are actively involved in both litter bag study and the planning for the long-term soil organic matter study. Our workshop on stable isotopes was also quite successful; it has led to a sharp increase in the use of stable isotopes at LTER sites.

A third intersite LTER workshop will be held in Woods Hole in September

1991, on soil warming experiments. Organized by Bill Schlesinger of the Jornada LTER, the aim of the workshop is to discuss the possible effects of soil warming at contrasting LTER sites, and perhaps to develop another inter-site experiment. We will be active participants, and in fact plan to do some preliminary studies in the field this summer.

Finally, one of the goals of our modeling program is to use our models to predict and compare the possible responses of contrasting ecosystem types to disturbances including global climatic change. Comparison of LTER sites in this context is a particularly attractive means of achieving this goal, and we have already begun. Our collaboration with the Harvard Forest LTER is particularly strong, since several of the HFR researchers are members of the Ecosystems Center and one, Knute Nadelhoffer, is on both LTER projects. We have already completed one paper comparing HFR with tussock tundra at Toolik Lake, and have succeeded in parameterizing our GEM model for several other LTER sites.

LTER GOAL I: ECOLOGICAL VARIABILITY AND LONG-TERM CHANGES

Terrestrial research

Can we detect long-term changes in the Arctic climate? Are terrestrial ecosystems changing in response?

These questions are being addressed through long-term monitoring and manipulation of both climate and key ecosystem processes. For example, growth and flowering of Eriophorum vaginatum, one of the most common and often dominant plant species throughout the Arctic, has been monitored at 34 sites along the climatic gradient between Fairbanks and Prudhoe Bay since 1976. At 14 of these sites small, factorial fertilizer experiments have been established, and at 6 sites reciprocal transplant gardens were set up in 1979 and 1980. Every year, at as many of these sites as possible, we count the number of inflorescences produced in permanent plots, estimate productivity using standard indices of leaf production and tillering, and analyze standard tissues for element concentrations.

The combination of these approaches has allowed us to distinguish the effects of annual variation in climate from broad regional differences in climate at two time scales: in the long-term, we can show that genetically-based, ecotypic variation between populations accounts for much of the variation in plant size and growth rate that we observe in the field, and that this variation is correlated with long-term average growing-season temperatures (Fig. 2). In the short-term, we can show that growth and especially flowering vary uniformly from year to year over most of Alaska (Fig. 3), but these annual fluctuations are not clearly correlated with annual variation in any climatic variable. Our results have led us to the conclusion that short-term plant responses to climate must be strongly "buffered", or constrained, by other limiting factors such as nutrient availability, and that longer-term responses are constrained genetically. Detection and explanation of multi-year trends in plant growth in relation to climate, then, requires linking climatic changes to changes in soil nutrient cycling processes and nutrient availability. Changes in element cycling in relation to climate, rather than direct climatic effects on plants, should determine long-term trends in plant growth and flowering. By now, our record of observations at some sites is long enough that effects of long-term, cyclic events such as El Nino-Southern oscillation phenomena should soon be evident though as yet they are not.

The consistent importance of nutrient limitation in determining both annual variation in productivity and long-term biomass accumulation of tundra plants has been shown clearly in our factorial fertilizer experiments. All 14 sites responded significantly to fertilizer addition, including sites in both wet sedge tundra and moist tussock tundra. Intriguingly, however, the specific elements that caused the responses were different in each site, and the responses of wet sedge tundras were not consistently different from the responses of moist tussock tundras -- in both vegetation types, some sites are N-limited and some are P-limited.

Our fertilizer experiments have also helped to reveal some of the mechanisms behind the lack of a simple relationship between annual climatic variation and annual variation in plant growth and flowering. Most importantly, it appears to take about 2-3 years for a growth response, and 3 years for a flowering response, to develop in response to fertilizer addition (Fig. 4). The probable reason for this slow response is that it simply takes time to develop and differentiate new vegetative and flowering meristems that can act as sinks for increased resource availability. This suggests to us that annual fluctuations in climate may, in effect, cancel each other out, and that large changes in growth and flowering should require two or more consecutive years of above- or below-average climatic conditions.

Lake Studies

What are the long term trends in primary productivity of arctic lakes and how are these trends related to potential climate changes?

We are currently monitoring 7 lakes for primary productivity, temperature, light penetration, water chemistry, and species composition. For Toolik Lake we have a 15 year record of dissolved nutrients, temperature, algal biomass, and primary productivity. Our monitoring program over this time span indicates that, in the context of climatic change, the master variable for controlling productivity appears to be temperature. Temperature regulates weathering rates, decomposition, and the depth of thaw in terrestrial ecosystems, all of which alter the flux of nutrients through terrestrial landscapes and into lakes. Temperature also regulates the strength and extent of thermal stratification and thus the zone of highest productivity in the lake. Under the present climatic regime, the amount of phosphorus entering the lake is also controlled by the amount of water entering the lake and it is the phosphorus quantity that controls algal primary productivity (Miller et al. 1986). Our best correlation so far is between primary productivity and water flow (Fig. 5). Our research is aimed at first documenting changes in the environment and biota caused by measured variations in climate, and second at modeling the response of productivity to future changes in temperature brought on by greenhouse warming.

Are there long-term changes in species composition?

Our longest record of changes in biota is from Toolik Lake, where increased fishing pressure during the last 15 years has had dramatic effects on the size structure and composition of fish populations. The average lake trout size declined from 578 g in 1977 to 318 g in 1986, and grayling have moved from close to shore into the open water because of reduced lake trout predation. As a consequence of more zooplanktivorous graying in the open water, large-bodied zooplankton species have declined dramatically, *Heterocope septentrionalis* by a factor of 2, *Daphnia middendorffiana* by a factor of 50, and Holopedium gibberum by a factor of 200 (Fig. 6). There is evidence that, in turn, the predatory Heterocope controls the abundance of small-bodied zooplankton. The smaller zooplankton in Toolik still seem to be facing severe predation pressure because Bosmina longirostis and Daphnia longiremis decrease in abundance throughout the summer whereas in other lakes in the area, which lack Heterocope, populations of these two species increase throughout the summer. Clearly we need to continue to monitor these populations in Toolik Lake.

Stream Studies

What is the variability in annual water discharge from the Kuparuk watershed and is there a discernible long-term trend in discharge possibly related to climatic change?

The flow of water through the landscape affects many key biogeochemical processes that will potentially change if the hydrologic cycle is significantly changed by either long-term trends or changing annual variability in discharge. For example, increased water flow will likely increase weathering rates of soils in the watershed and increase the export of dissolved cations, anions, nutrients and dissolved organic materials from land to rivers and lakes. Higher discharge will also lead to greater streambank erosion which captures peat. When discharge is low, the flux of materials from land to water is decreased and the balance between autotrophic and heterotrophic processes in streams and lakes is probably shifted in favor of autotrophy. If climatic change does change either the amount of water flow through arctic watersheds or the timing of these flows, we expect large changes in nutrient fluxes and in biotic activity in rivers, lakes, and estuaries. Our monitoring program is designed to document these changes.

Mean summer discharge over the last 8 years has varied from a low of 0.32 m^{-3} sec^{-1} in 1990 to a high of 3.8 m^{-3} sec^{-1} in 1984 (Fig. 7). These differences have been accompanied by equally large differences in primary production, insect abundance and grayling growth, some of which are probably related to discharge. Primary production of epilithic algae can be set back by removal during high summer discharge events (Fig. 8). But black flies may do well during high flow years when allochthonous organic matter fluxes are high (Fig. 9). On the other hand larval fish growth is poor during high discharge summers while adult grayling do well (Fig. 10). These relationships are only beginning to emerge from our studies to date but it is clear that climatic factors are affecting all chemical fluxes and all trophic levels in the river. Climatic effects are also having a substantial impact on the response of the river to phosphorus enrichment.

LTER GOAL II: CONTROL BY RESOURCES VS. CONTROL BY GRAZING AND PREDATION

Terrestrial Studies

What is the relative importance of changes in air temperature, changes in light intensity (due to changes in cloudiness), and changes in soil nutrient availability on terrestrial ecosystems, and how might these changes interact?

In a series of short- and long-term experiments that began in 1976, we have manipulated air temperature by building small greenhouses over the tundra, light intensity by shading, and nutrient availability by fertilization. Thus far, we have shown that changes in nutrient availability have effects on productivity and composition of tundra vegetation that are far greater than changes in either air temperature or light. In fact, productivity and plant biomass accumulation are quite closely tied to whole-plant nutrient content (Fig. 11, 12; Table 4). The main effect of increased air temperature is to speed up the changes due to fertilizer alone. Without fertilizer the effect of increased temperatures on the vegetation is slight even after 9 years, and probably results from small increases in soil temperatures and increased nutrient mineralization.

These results are consistent with results of our monitoring studies, and again lead to the prediction that effects of climate change on nutrient cycling processes are the key to understanding climate change in the Arctic. The Arctic is also one of the few natural systems where such whole-ecosystem experiments on terrestrial ecosystems are possible, due to the low stature and fine-grained heterogeneity of the tundra vegetation. Because the number of species in the vegetation is small, both the responses of individual species and of the whole vegetation can be determined and compared. A new, more extensive series of experiments was set out in four contrasting vegetation types in 1989.

Our field experiments have been complemented by laboratory experiments on key processes. For example, one of our most successful laboratory experiments involved incubating soils from six contrasting tundra ecosystems at three temperatures, in order to determine effects of temperature on soil respiration and N and P mineralization. At a given temperature, there was a threefold variation in respiration rate among the soils, and up to a tenfold variation in N and P mineralization rates (Fig. 13). These intersite differences were in general greater than the differences in respiration or mineralization rates due to temperature changes for a given soil. By comparison with temperate soils, our arctic soils had relatively high respiration rates and low N and P mineralization rates (Table 5), suggesting relatively high microbial demands for these elements and helping to explain the very low mineralization rates and strong nutrient limitation of plant growth that we have observed in the field.

Recently we have begun to realize that not only the total amounts of N and P made available to plants, but also their specific molecular forms, are critical to understanding vegetation patterns and productivity. In a survey of the N stable isotopic ratios ($\delta^{15}N$) in leaves of various tundra plant species, we found a remarkably wide range of $\delta^{15}N$ values (Table 6), suggesting that N gets into these plants by a number of different pathways or as NH_4 versus NO_3. The differences between species are also consistent across sites (Table 7); graminoids like Eriophorum vaginatum and Carex Bigelowii are consistently enriched in ^{15}N, by about 4-6°/$_{oo}$, than deciduous birch or willow species, with ericads like Ledum palustre consistently being the most depleted in ^{15}N. Forb species are more variable, although deep-rooted forbs tend to be more enriched in ^{15}N than shallow-rooted forbs. We can envision several possible explanations for these consistent patterns, involving at least three factors: (1) mycorrhizal versus nonmycorrhizal N uptake, (2) type of mycorrhizae responsible for the uptake, and (3) rooting depth.

The results of our experiments have led us to develop an overall conceptual model of carbon and nutrient interactions at the whole ecosystem level, which we are currently using to guide our research (Fig. 14). In the model, linkages between the carbon and the nitrogen cycles occur through controls over the C:N ratios in plant and soil organic matter, and over the ratios of the fluxes of C and N into and out of these pools (the "bow ties" in

Table 4. Total biomass (excluding roots) and its N and P content, and Net Primary Production (NPP) and its N and P content, in four common tundra vegetation types near Toolik Lake, Alaska (from Shaver and Chapin 1991). The right-hand column, headed "Variation", indicates the range of variation among sites as the quotient of the largest value in each row divided by the smallest value. The main point here is that intersite variation on biomass and NPP is accompanied by a nearly proportional variation in N and P mass, with relatively little change in overall element concentrations, especially of N.

	Moist Tussock Tundra	Riparian Shrub Tundra	Wet Sedge Tundra	Evergreen Heath Tundra	Variation
Total Biomass ($g \cdot m^{-2}$)	856	1878	438	207	9X
N in biomass ($g \cdot m^{-2}$)	8.15	14.66	4.37	1.84	8X
P in biomass ($g \cdot m^{-2}$)	0.86	1.05	0.84	0.13	14X
% N in biomass	0.9	0.8	1.0	0.8	1.3X
% P in biomass	0.10	0.06	0.19	0.06	3.2X
NPP ($g \cdot m^{-2}$)	158	305	69	32	9.5X
N in NPP ($g \cdot m^{-2}$)	2.33	4.40	1.09	0.42	10.5X
P in NPP ($g \cdot m^{-2}$)	.239	.285	.161	.031	9.2X
% N in NPP	1.5	1.4	1.6	1.3	1.2X
% P in NPP	0.15	0.09	0.23	0.10	2.3X

Table 5 Element mineralization ratios in 13-week incubations of soils of six arctic ecosystems near in the foothills region of the North Slope near the Sagavinirktok River, Alaska.

Site	Horizon	C:N mineralized g/mg			C:P mineralized g/mg			N:P mineralized g/g		
		3°C	9°C	15°C	3°C	9°C	15°C	3°C	9°C	15°C
Tussock Tundra	Oe+Oa	0.68	0.91	0.55	8.4	59.5	220.9	12	65	400
Hilltop Heath	Oe+Oa	3.97	1.72	2.80	19.1	43.1	45.4	5	25	16
Hillslope Shrub/Lupine	Oe	2.43	2.95	2.22	15.2	36.4	68.7	6	12	31
	Oa	2.11	1.98	0.56	12.9	10.1	64.7	6	5	115
Footslope Equisetum	Oe	4.65	3.10	2.30	94.8	180.2	50.5	20	58	22
	Oa	1.34	0.83	0.40	22.8	7.3	18.5	17	9	46
Wet Sedge Tundra	O	0.14	0.12	0.16	8.6	20.3	143.9	62	168	919
Riverside Willow	Oe+Oa	1.86	0.66	0.12	23.4	9.2	10.3	13	14	85
	C	2.34	1.61	0.51	17.8	10.4	40.6	8	6	80
	IIO	0.08	0.04	0.04	0.2	0.4	1.2	2	10	36

Table 6. $\delta^{15}N$ values in leaves of tussock tundra plants, at two sites in northern Alaska.

	Sag River	Toolik Lake
Sedges		
E. vaginatum	0.4 - 2.7	1.5 - 4.8
C. bigelowii	1.2 - 2.9	
Deciduous Shrubs		
Salix	-4.2 - -4.7	-3.7 - -4.0
Betula	-5.7 - -7.1	-5.8
Ericads		
Vaccinium	-7.1, -7.2	
Ledum	-7.8	
Cassiope	-8.1, -8.8	
Mosses		
Hylacomium	-2.7	
Aulacomnium		-1.9, -2.4
Sphagnum	-2.8, -2.9	-1.7, -2.1
Forbs		
Rubus		0.7 - 0.9
Polygonum		0.3 - 1.0
N-fixers		
Lupine	-0.2, 0.0 (Site 4)	
Alder	-1.5 (Site 3)	

Table 7. $\delta^{15}N$ values in leaves of *Eriophorum vaginatum* and Betula nana, at 9 sites between Fairbanks (-Smith Lake) and Prudhoe Bay, Alaska.

	E. vaginatum	*B. Nana*
Smith Lake	2.2, 2.9	
Eagle Creek	0.5, 1.0	
Coldfoot	0.9, 0.7	
Snowden	2.1, 2.6	-5.9, -6.2
Timberline	1.2	-7.4, -4.1
Toolik Lake	1.5, 4.8	-5.8
Sag River	0.4, 2.7	-5.7, -7.1
Sagwon	1.7, 2.1	
Prudhoe Bay	2.3, 3.6	

Fig. 14). The actual values for the C:N ratios indicated in the boxes are typical of wet and moist tundra ecosystems, but could be much higher in other ecosystem types, especially in forests where woody biomass may have a C:N ratio of 200 or more. The basic idea, however, is generally applicable; that is, all pools and fluxes of organic matter must contain both C and N, and the ratios of these elements are not infinitely flexible.

All of the evidence reviewed above is consistent with the idea that large, long-term changes in tundra carbon cycling will be tightly constrained by changes in the cycling of other elements. Because plant C accumulation in the tundra at Toolik Lake is strongly N-limited, a sustainable increase in C accumulation requires a sustainable increase in N uptake (other tundras are P-limited). Environmental changes that do not directly affect the N cycle will be constrained in their effects on the C cycle by constraints on C:N ratios.

How do the soil and plant responses to climate change affect terrestrial herbivore populations, and do feedbacks due to herbivory affect soil and plant responses?

This question has not been addressed in previous terrestrial research at Toolik Lake, but our new experimental series includes herbivore exclosures to be used in the search for an answer. These experiments were set up in 1989; they will be sampled at least every 3-4 years over the next 10-15 years.

Lake Studies

How much is the structure and function of the lake ecosystem controlled by resources (bottom up control), such as the rate of nutrient input, and how much by grazing and predation (top down control)?

To isolate the effects of nutrient availability on productivity we initiated process oriented studies on the effects of fertilization. These studies began in 1983 using large limnocorrals and have been expanded to whole systems with our current experiments in divided lakes. The summer of 1990 was the last of 6 years of nutrient fertilization in the divided Lake N-2. During this period there were large increases in phytoplankton biomass and snail numbers and growth in the fertilized side of the lake (Fig. 15). The zooplankton, fish, and other benthos responded either with a 1 to 2 year time lag, or not at all, which is consistent with our previous results and with several other fertilization studies in arctic and temperate lakes (see Appendix II for a fuller description). Much of the phosphorus added to the lake was tightly bound to the iron-rich sediments, and was not recycled to overlying waters under aerobic or anaerobic conditions. This iron-bound PO_4 is apparently available only to benthic algae, and we measured a 2 to 3 fold increase of benthic algal productivity in the fertilized side of Lake N-2. This phenomenon of strong nutrient binding in sediments should allow for a rapid recovery from lake eutrophication caused by external nutrients. We will test this prediction by ceasing to fertilize Lake N-2 starting in 1991 and measuring the recovery rate of water chemistry and biota to the pre-fertilization conditions. Last summer we replaced the old curtain that divides the lake in half, and so the integrity of the experiment will be retained in the following years.

A replication of this fertilization experiment was started in 1990 in nearby Lake N-1. One advantage of Lake N-1 is that it contains grayling as well as the top predator lake trout, whereas Lake N-2 contained only grayling. The addition of nutrients to Lake N-1 will thus allow us to look at the effects of fertilization on higher trophic levels when the top predator is present, and to better define the interaction between bottom-up and top-down controls. For example, predation by lake trout, in combination with resource competition, seems to limit snail populations in these lakes. When lake trout are absent, snails are very abundant and fertilization stimulates their growth and increases their numbers, as occurred in Lake N-2. In 1990 we also measured an increase in snail growth in exclusion cages in Lake N-1, but whether the population sizes of snails will increase as well in a fertilized lake containing lake trout can only be determined by continuing the long-term enrichment study.

To investigate the higher trophic levels and their controls on populations below them we have been both monitoring and experimentally manipulating a series of lakes. The experimental manipulations of top predator populations include a slow removal of lake trout from Lake I-8, a fast removal of lake trout from Lake NE-12, and the introduction of lake trout to Lake S-6 (Table 2). The most striking result so far is a change in the distribution of the bottom dwelling sculpin and predaceous burbot in response to complete removal of lake trout from Lake NE-12. We had expected that in the absence of predation pressure, sculpin would move away from the rocky shallows and out onto the soft sediment where food availability is higher. Instead, sculpin moved even more toward the rocky shallows after the lake trout were removed (Fig. 16). We also measured a large number of burbot moving from deep in the lake, where they can most easily avoid predation by lake trout, into the nearshore zones. This large increase in burbot in the shallows drove the sculpin away from the soft, exposed sediment, and apparently the control of sculpin by burbot predation is even stronger than was the control of sculpin by lake trout. We will continue to monitor these behavioral responses to changing predator populations in 1991.

Our experimental designs have allowed us to test the interaction of bottom-up and top-down controls at the ecosystem scale. For example, at the level of fertilization we applied to Lake N-2, the chironomids did not respond even after benthic algal productivity had more than doubled. We conclude that predation by sculpin is intense enough to maintain chironomid densities below the level at which they would be food or resource limited. A corollary of this is that lake trout will not obtain extra food from sculpin during eutrophication of these lakes. This important finding requires more work and confirmation in other lakes. We will continue the fertilization of Lake N-1, which contains chironomids, sculpin, and lake trout, and beginning in 1991 we will add sculpin to Lake E-1 (no sculpin, abundant chironomids) and remove sculpin from Lake N-3 (sculpin, few chironomids) to test the intensity of the linkage and of the controls.

So far the results of our experiments indicate that both bottom-up and top-down controls operate simultaneously and are important in these ecosystems; rarely is there a single master variable that constrains the structure of all populations or the processes involving nutrient and carbon flow. Our current understanding of resource controls and feedback effects in lake food webs is presented in more detail in Appendix II and depicted in Figure 1 of that Appendix.

<u>Stream Studies</u>

<u>If climate change accelerates chemical weathering and phosphorus export</u>

from the tundra, how will the life of streams and rivers be changed? How much is the ecosystem controlled by resources (bottom-up) vs. predation (top-down) control?

An overview and synthesis of the response of the Kuparuk River biota to the addition of phosphorus is given in Fig. 17. The bottom-up effects of nutrients as they propagate through the ecosystem are diagrammed flowing from left to right. The top-down or feedback effects are diagrammed flowing from right to left. The steps are numbered and described in the following paragraph.

The sequence of responses that we have measured over the past seven years is as follows (numbers in parentheses refer to Fig. 17): dissolved phosphate added to river water stimulates the growth of epilithic algae (1) (Fig. 18). Increases in algal production lead to sloughing and export of algal biomass and increased excretion and mortality. Increased algal excretion and mortality stimulate bacterial activity which is also stimulated directly by phosphorus addition (2, 3). Increased bacterial activity and biomass make possible an increase in the rate of decomposition of refractory compounds such as lignocellulose and many components of the DOM pool (4). The increases in algal and bacterial biomass provide increased high quality food for filtering and grazing insects (5, 6). The insects respond with increased growth rate and, in the case of Baetis and Brachycentrus, with increases in density. However, Prosimulium density in the fertilized reach declines due to competitive interaction with Brachycentrus (7). The increases in insects other than Prosimulium increase the available food for grayling; both young-of-the-year and adult grayling grow faster and achieve better condition in the fertilized reach (8). In the long-term, if the experimental nutrient addition were expanded to include the whole river and barring other overriding but unknown fish population controls, we hypothesize that the fish population would increase (9). If so, it is possible that predation by fish would exert increased top-down control over insects such as Baetis or Brachycentrus which are vulnerable to fish predation when drifting and emerging (10). Experimental evidence from bioassays using insecticides indicates that grazing insects control algal biomass (11) (also, in Fig. 18 the low algal biomass in 1985 and 1986 is due to growth and grazing of insects). Finally, increases in epilithic algae and bacteria are responsible in part for uptake of added phosphorus and ammonium and for uptake of naturally abundant nitrate (12). Thus, the bottom-up effects of added nutrients are paralleled by several top-down effects of fish on insects, insects on insects, insects on epilithic algae, and epilithon on dissolved nutrient levels.

In summary, the entire biological system in the river is responsive to added phosphorus. The bottom-up effects propagate to all levels in the food web. Also both top-down effects and competitive interactions are clearly important in the response of the ecosystem to fertilization.

LTER GOAL III: RATES AND CONTROLS OF THE EXCHANGE OF NUTRIENTS AND ORGANIC MATTER BETWEEN LAND AND WATER

The question of land-water interactions is fundamental to our understanding of terrestrial and aquatic ecology and to predictions of climate change on arctic ecosystems. At the Toolik Lake site we already have a great deal of small plot measurements of nutrients in soil water and their interactions with plants. There are also large-scale data on the flux of nutrients and organic matter out of entire watersheds. Much information exists on the response of aquatic organisms to the inputs of nutrients from land. We have begun to study intensively the effects of riparian zones on nutrient transformations, as well as the flux of dissolved inorganic and organic carbon from land to water. In the next few years we will construct a dynamic model of the movement of nutrients into streams and combine this with a Geographic Information System (GIS) to account for the variability within and between watersheds.

What controls the flux of nutrients and water over the arctic landscape and into aquatic ecosystems?

In this research our principal aim is to evaluate the magnitude and relative importance of lateral N and P fluxes in soil water moving across the surface of the permafrost, between terrestrial ecosystem types, and from terrestrial to aquatic systems. Our most intensive study site is a toposequence of six contrasting ecosystem types in the Sagavanirktok River valley about 40 km northeast of Toolik (Fig. 19). To estimate N and P fluxes in soil water at this site we have had to develop and compare overall N and P budgets for all six ecosystems, and to link these budgets with a hydrologic model.

One of our major conclusions so far is that the net uptake per square meter of N or P from moving soil water is small relative to internal fluxes like annual plant uptake or N mineralization. However, each of the six ecosystem types has a major and very different effect on the total amounts of NO_3, NH_4, and PO_4 in the soil water (Table 8). This has very important implications for the inputs of these nutrients to aquatic systems. Some ecosystem types, like tussock tundra and dry heath, are major sources of N to soil water. Other systems, particularly those occurring under or below late-lying snowbanks, are important N sinks and P sources to soil water. Poorly-drained wet sedge tundra is a P sink with a remarkably high N mineralization rate.

We have also learned a great deal about patterns and controls over N and P cycling processes along the toposequence. Among our most important discoveries, we have shown that nitrification (conversion of ammonium to nitrate) is much more important along the toposequence than we suspected based on earlier research, and many plant species show high nitrate reductase activity. We also have strong evidence from stable isotope analyses that different plant species are using isotopically different N sources, and that these species differences are maintained across sites. The relative amounts of different forms of organic and inorganic P in soils also vary dramatically across sites.

In summary, our work has shown that different terrestrial ecosystems differ strongly in their chemical interactions with the soil water, and thus have highly variable effects on the chemistry of water entering aquatic systems. This work is important in the context of global change, because if either the composition of the landscape mosaic changes, or the biogeochemistry of individual landscape units changes, the chemistry of inputs to aquatic systems should also change. Combined with our new series of whole-system experiments, we should eventually be able to develop predictions of these changes, and thus predict changes in nutrient inputs to lakes and streams.

What are the effects of riparian zones on nutrients?

Our focus here has been on the extent of nutrient transformations as water flows through the riparian zone and into streams and lakes. The hypo-

Table 8. Calculation of net inorganic N and P exchange by each ecosystem type. "Cumulative l H_2O" is the estimated volume of water that passes out the bottom of each ecosystem from a 1 m wide transect starting at the top of the tussock tundra, assuming a net annual water input of 75 $l \cdot m^{-2}$ (75 mm) along the transect. "Total output is equal to this cumulative water volume times the 3-year average concentration.

	Mean Concentration in soil water, ug/l[a] 1986	1987	1988	avg.	Horizontal Distance, m	Cumulative l H_2O/yr	Total output, mg/ecosystem/yr
A. Nitrogen							
Tussock tundra	259	140	249	216	50	3750	810
Hilltop heath	272	172	300	248	10	4500	1116
Hillslope shrub/lupine	91	81	190	121	20	6000	726
Footslope *Equisetum*	34	49	195	93	10	6750	628
Wet sedge tundra	102	162	232	165	30	9000	1485
Riverside willow	169	87	182	146	-	-	-
B. Phosphorus							
Tussock tundra	37	13	15	22	50	3750	83
Hilltop heath	27	11	18	19	10	4500	86
Hillslope shrub/lupine	30	10	10	17	20	6000	102
Footslope *Equisetum*	30	11	18	20	10	6750	135
Wet sedge tundra	16	9	5	10	30	9000	90
Riverside willow	18	11	12	14	-	-	-

[a] From Giblin et al. (in press)

rheic (deep-flowing) zone beneath streams also plays a role in delivering and transforming the nutrients.

Pilot studies of the riparian zone have shown that there is frequently active nitrification in the deeply thawed creekbank willow zone (Fig. 20). Water seeping downslope was high in ammonium entering this zone but this ammonium was rapidly converted to nitrate in the last few meters before seeping into the river. We also know from our whole river ammonium addition that nitrification is very active in the river channel as well. Preliminary chemical data from the hyporheic zone water, collected from stainless steel tubes driven into the stream bottom, suggest that water in this layer is derived from lateral seepage and is not simply river water. There may be also some nitrification as water with high ammonium concentrations moves from the hyporheic zone upward and closer to the river channel.

In 1990 we established a small experimental watershed close to Toolik Lake for further investigation of nutrient transformations as water moves from land to lakes and streams. By measuring nutrients in soil waters across a transect from upland tundra to the riparian zone, we have confirmed the pilot studies that suggested active nitrification occurred near the lake and stream edge. The lower part of the experimental watershed contains an area underlain by galcial material that is only about 15,000 years old, compared to the 100,000 year old material covering the upper watershed. Because the age of the land surface controls the extent of weathering, there are large differences between young and old areas in the amounts of major ions draining into surface waters. Our preliminary results indicate that nutrient export may be affected by landscape age as well. In addition to this spatial variability in nutrient concentrations and forms, we have also detected strong seasonal trends in the concentrations of nutrients draining from tundra soils.

How does the flux of dissolved inorganic and organic carbon from lakes to rivers affect changing carbon balance in the Arctic?

We have shown that the flux of inorganic carbon from tundra to lakes and streams is much greater than anyone had anticipated. In general, the lakes and streams of the North Slope examined by us are supersaturated with CO_2 and thus they continuously release CO_2 to the atmosphere. Measurements of the pCO_2 of soil waters in our experimental watershed and selected sites in the Kuparuk watershed during 1990 showed an even greater supersaturation; this leads us to believe that the excess CO_2 comes from decomposition in tundra soils and moves into streams and lakes in groundwater. The magnitude of CO_2 release from lakes and streams to the atmosphere is 20-50% of the estimated value for terrestrial net primary productivity of the tundra. The implications of this finding are that first, previous net primary productivity numbers based on CO_2 exchange in terrestrial sites were too high because the loss of terrestrially fixed carbon through aquatic systems was not accounted for. Second, the large release of carbon gases to the atmosphere, that is projected under a scenario of temperature increases in the Arctic, will be augmented by CO_2 evasion from lakes and streams. We do not know, however, how much of the release from lakes and streams actually comes from the CO_2 in soil water and how much comes from in-lake decomposition of organic matter originating from the land. Beginning in 1991 we will gauge the export of water from the experimental watershed, and measure how much dissolved organic matter (DOC and DON) from soils enters the lakes and streams.

Our experimental watershed has been mapped for vegetation, soils, and landforms at the 1:1000 scale. This information, along with the results from the monitoring of soil water chemistry and flow, will be incorporated into our modeling approach and the GIS system we have developed for the Toolik LTER (see below).

While the response of aquatic organisms to dissolved nutrients input from land is well understood, the response to particulate material washed in from the tundra is less clear. In some high latitude lakes, for example, the zooplankton make their living directly on inputs of terrestrial detritus rather than from the phytoplankton in the water column. We tested the importance of this linkage between lake organisms and inputs of particulate material from the tundra by adding tracer amounts of $^{15}NH_4Cl$ to both the control and the fertilized sides of Lake N-2 in order to label the phytoplankton. The terrestrial detritus remained unlabeled with ^{15}N. The ^{15}N label appeared in the algae almost immediately, and their ^{15}N content increased steadily over the summer. By the end of the summer, the ^{15}N content of zooplankton was similar to that of phytoplankton in both sides of the lake (Fig. 21). This similarity in ^{15}N content shows that the pelagic food web is dependent on new algal production within the lake rather than on terrestrial detritus washed into the lake.

SYNTHESIS: COMPARATIVE STUDIES

Lake and Stream Survey on North Slope Transect

As part of an effort to extrapolate our data and understanding to the regional scale, we have measured physical, chemical, and biological variables at a variety of aquatic sites on the North Slope. In 1990 we completed a survey of 45 lakes and 7 streams along a 230 km transect from the Brooks Range north to the Arctic Ocean. Variations in water chemistry among the sites were related to differences in bedrock and the age of associated glacial drift, while variations in species composition were related mostly to biotic interactions. These surveys will continue in 1991, and will concentrate on determining how widespread is the phenomenon of strong nutrient binding by the sediments that we observed in the Lake N-2 fertilization experiment.

Growth and Flowering Transects of *Eriophorum vaginatum*

Earlier in this document we described how growth and flowering of *Eriophorum vaginatum*, one of the most common and often dominant plant species throughout the Arctic, has been monitored at 34 sites along the climatic gradient between Fairbanks and Prudhoe Bay since 1976 (see Fig. 3). At 14 of these sites small, factorial fertilizer experiments have been established, and at 6 sites reciprocal transplant gardens were set up in 1979 and 1980. Every year, at as many of these sites as possible, we count the number of inflorescences produced in permanent plots, estimate productivity using standard indices of leaf production and tillering, and analyze standard tissues for element concentrations.

The combination of these approaches has allowed us to distinguish the effects of annual variation in climate from broad regional differences in climate at two time scales: in the long-term, we can show that genetically-based, ecotypic variation between populations accounts for much of the variation in plant size and growth rate that we observe in the field, and that this variation is correlated with long-term average growing-season temperatures

(Fig. 2). In the short-term, we can show that growth and especially flowering vary uniformly from year to year over most of Alaska (Fig. 3), but these annual fluctuations are not clearly correlated with annual variation in any climatic variable.

Soil and Nutrient Studies: Sagavanirktok Site vs. Toolik and R4D Sites

In these studies, we have already compared the results of studies of the toposequence of six contrasting ecosystem types in the Sagavanirktok River valley about 40 km northeast of Toolik (Fig. 19) and are now comparing these toposequence results with those from studies of the Toolik and Kuparuk (R4D site) regions.

One of the major conclusions from the comparative study at the Sagavanirktok site was the realization that nutrient removal from moving soil water is small relative to internal fluxes like annual plant uptake or N mineralization. Also, each of the six ecosystem types has a major and very different effect on the total amounts of NO_3, NH_4, and PO_4 in the soil water (Table 8). Nitrification is much more important along the toposequence than we suspected based on earlier research, and many plant species show high nitrate reductase activity. We also have strong evidence from stable isotope analyses that different plant species are using isotopically different N sources, and that these species differences are maintained across sites. We are now examining how closely the ecosystems at the other sites follow this pattern.

Comparisons Among LTER Sites

The EPA funded project described earlier is measuring CO_2, CH_4 and N_2O emissions at both the Arctic LTER and the Bonanza Creek LTER sites. This project will make use of the long-term manipulated plots of nutrient, shade, and warming.

A comparative project is also underway to test the effect of manipulation of litter inputs on long term accumulation and cycling of soil organic matter. The Arctic site is taking part and we are actively involved in both litter bag studies and the planning for the long-term soil organic matter study.

An intersite LTER workshop will be held in Woods Hole in September 1991, on soil warming experiments. Organized by Bill Schlesinger of the Jornada LTER, the aim of the workshop is to discuss the possible effects of soil warming at contrasting LTER sites, and perhaps to develop another intersite experiment. We will be active participants, and in fact plan to do some preliminary studies in the field this summer.

One of the goals of our modeling program is to use our models to predict and compare the possible responses of contrasting ecosystem types to disturbances including global climatic change. We have already completed one paper comparing Harvard Forest stands with tussock tundra at Toolik Lake, and have succeeded in parameterizing our GEM model for several other LTER sites.

SYNTHESIS: MODELING AND SCALING UP

Modeling of Tundra Biogeochemistry

With funding from NSF-BSR, a group at the Ecosystems Center has developed a general biogeochemical model of the responses of terrestrial ecosystems to changes in atmospheric CO_2 concentration, climate, and nutrient inputs. For the LTER research we are using this model, called the Generic Ecosystem Model or GEM, to interpret, synthesize, and extrapolate the results of our plot-based studies of tundra biogeochemistry.

The Biogeochemical Model. The existing model is a highly-aggregated, process-based, biogeochemical model designed to examine changes in the fluxes and allocation of carbon and nitrogen among foliage, fine roots, stems, and soils in response to changes in atmospheric CO_2 concentration, temperature, soil moisture, irradiance, and inorganic nitrogen inputs (Fig. 22). GEM was developed on the principle that the responses of terrestrial ecosystems to changes in CO_2, climate, and N deposition will encompass kinetic responses of enzymes, stoichiometric shifts in tissue C to N ratios, changes in the allocation of plant biomass among tissues, altered rates of soil organic matter turnover and N mineralization, and ultimately a redistribution of C and N between vegetation and soils. The model is a rigorous effort to examine the interactions and inter-dependencies of all of these processes.

The model simulates changes in the amounts of C and N in several vegetation tissues and in four soil organic fractions, as well as the amount of soil inorganic nitrogen. Within the vegetation, both labile (readily mobilized) and structural (including enzymatic machinery and structural framework) components of foliage, stems, and fine roots are represented. For woody vegetation, the amounts of C and N in heartwood is also simulated. Younger soil organic matter including litter is divided into "extractives" (extractable in methylene chloride and hot water), "cellulose" (acid soluble fraction of remaining residue), and "lignin" (acid insoluble fraction). Older organic matter is converted to humus. The equations describing the movement of C and N among these variables are based on the known or hypothesized physiology of the metabolic processes involved. The model is designed so that the same model structure can be easily applied to the different types of vegetation found in the tundra by recalibrating the model parameters.

We have used this model to examine the responses of moist tundra to changes in CO_2, temperature, and N input and have compared these results to similar simulations for hardwood forests (Fig. 23). The model was first calibrated to simulate present stocks and turnovers of carbon and nitrogen at the Arctic and Harvard Forest Long-Term Ecological Research sites. We then ran simulations to examine responses to a doubling of atmospheric CO_2, a five-degree C temperature rise, and an increase in N deposition.

One of the assumptions of the model is that the cycling of nitrogen and carbon is always linked; organic matter created during photosynthesis and destroyed during decomposition always contains both nitrogen and carbon in relatively restricted ratios. For this reason, we were not surprised that the model simulations indicated that sustainable responses in production and biomass accumulation to any of these changes are strongly bounded by rates of nutrient recycling through soils (Fig. 23). The two ecosystems have qualitatively similar responses. The small quantitative differences can be attributed to differences in the initial distribution of carbon and nitrogen between plants and soil organic matter and to differences in the amounts of wood in these two ecosystems.

In both ecosystems, linkages between the carbon and nitrogen cycles constrain responses to perturbation. Because the amounts of nitrogen imported from outside these ecosystems are so small relative to the nitrogen recycled internally, both ecosystems are limited in their ability to respond to perturbations by their ability to redistribute existing nitrogen within the ecosystem. The ability of these ecosystems to sequester carbon is therefore limited by their ability to move nitrogen from components with low ratios of carbon to nitrogen, such as soils and leaves, to components with high ratios of carbon to nitrogen, such as wood.

After a 50-year simulation, the sustained responses to increased CO_2 are relatively minor because of nitrogen limitation. Sustained responses to increased temperature are much larger. They lead to an increase in the nitrogen cycling rate through soils and a shift in nitrogen from the soil into the plants. When both CO_2 and temperature are increased, the responses are dominated by the temperature effect on nitrogen cycling. Responses of vegetation to nitrogen fertilization are constrained by the immobilization of nitrogen in soil organic matter.

The overall similarities in the responses of these two ecosystems are probably associated with the large stocks of soil organic matter in both, the slow turnover of these stocks, and their dependence on the internal distribution of nitrogen.

Modeling population structure and behavior of aquatic organisms

We have developed two models of aquatic organisms to help evaluate our experimental and survey results. Our bioenergetics model predicts the growth of lake trout feeding on snails and other fish. This model, applied to our arctic lakes, accurately simulates the change in growth pattern that occurs in some individuals as they shift from feeding on snails to piscivory. This shift is not universal, however, and some individual lake trout feed on snails throughout their lives. Our model results indicate that there are severe constraints to lake trout growth unless there is an adequate forage fish available. We plan to test this prediction by adding a forage fish such as cisco to a lake with lake trout.

We have also developed models of the feeding of arctic grayling on zooplankton in lakes and drifting insects in streams. The zooplankton feeding model predicts quite accurately the decline of large-bodied zooplankton that we have measured in Toolik Lake. By using the stream model, we can determine the favored distribution of grayling in the stream depending on stream velocity, and these distributions are consistent with observations in the arctic as well as in other systems. We are also using this model to help understand the impact of predation on population regulation of drifiting insects. Depending upon assumptions of drift distance and frequency, there may be little or no impact of predation on drifting insects.

FUTURE PLANS

Terrestrial research

A major goal for the future is to integrate the terrestrial research more closely with the aquatic studies, through the land/water interactions research described below. We also plan to continue our experimental research on top down/bottom up controls of tundra structure and function, with a particular emphasis on (1) processes affecting or dependent on element transport over the tundra landscape, and (2) carbon/nutrient interactions as controls on terrestrial carbon budgets. Both these efforts are essential if we are to be able to scale up our research to be able to predict both nutrient inputs to aquatic systems and CO_2 and methane exchange of complex landscapes.

<u>Soil Warming Pilot Study</u>: During the summer of 1991 we will initiate a pilot study of the effect of soil heating. The justification for a soil heating experiment is that the microbial processes in the arctic soils appear to be relatively independent of the actual soil temperature as long as the temperature range is within normal limits. When the overall temperature becomes higher than this normal range, which may happen during some disturbance or climate change, then there may well be a strong increase in the rates of microbial processes and a strong release of trace gases to the atmosphere. During the summer of 1991 we will install a 3 m x 3 m grid of heating wires and change the temperature of the soil by 5°C. The design and controls will be the same as those recently installed in a soil heating experiment at the Harvard Forest LTER site. The arctic experiment is a pilot study to see how the design works for arctic soils.

Aquatic research

One of the recurring observations of our monitoring, survey, and experimental work is that fish presence or absence in large part determines the species composition, the population sizes, or the spatial distribution of other lake organisms. This powerful structuring force is in turn regulated by, among other things, the morphometry of the lake basin; shallow lakes have too little water to sustain fish beneath the winter ice cover. Because deep lakes have a greater thermal capacity than shallow lakes, the ice cover of deep lakes thaws more slowly in the spring. As viewed from the air, this phenomenon creates a patchwork of varying amounts of ice cover on lakes at any given time during spring thaw. We plan to use this proxy for lake depth in order to predict the distribution of fish and the composition of aquatic food webs across large regions of the North Slope that would be impossible to survey by foot, and too expensive by helicopter. We have ordered a series of Landsat and SPOT satellite images covering the period of spring thaw on parts of the North Slope that we will incorporate into our developing GIS system. Such time series information from remotely sensed data also has the capability to resolve broad scale differences in the thermal regime of lakes on the tundra, and to apportion these differences into natural variability versus real trends brought about by climate change.

Our plans for future research also include the development of more specific models of lake response to climatic change. For example, we know that a critical variable for controlling lake productivity is temperature. Temperature regulates weathering rates, decomposition, and the depth of thaw in terrestrial ecosystems, all of which alter the flux of nutrients through terrestrial landscapes and into lakes. Temperature also strongly regulates the strength and extent of thermal stratification; the density structure of the water column determines what part of the lake receives nutrients from inflowing water, and thus defines the zones of highest productivity in arctic lakes. We will collaborate with the Northern Lakes LTER site in the use of one-dimensional lake models developed by Jorg Imberger and others (DYRESM) that predict the density structure of the water column and physical circulation of the lake given simple climatic information. We will then combine these model results, as has been done by the Northern Lakes group, with, for example, our model of fish bioenergetics. This approach of linking physical and biological models will allow us to predict the responses of plant and animal populations under a suite of anticipated or potential scenarios of climate change.

<u>Controls of the Microbial Food Web</u>: In 1991 we will conduct an experiment to determine first how much of the large amount of DOC and DON that comes from land is used by lake organisms, and second what controls the numbers of bacteria and the rates of bacterial decomposition within the ecosystem. The experimental design parallels our bottom-up and top-down approach to the food web involving larger animals; we will manipulate dissolved nutrient supplies and measure the effects of predation and grazing on bacterial communities. The top-down aspects will be coordinated with Dr. Parke Rublee, who has funds from the Division of Polar Programs for studying the microzooplankton in the Toolik Lake area.

Inputs of DOC and DON are probably very important to the aquatic ecosystems in the Arctic. For example, about 88% of the total nitrogen input to Toolik Lake is in the form of DON. If the measured amount of DON is really transformed into inorganic N and made available to algae, it would supply 75% of the nitrogen needed for photosynthesis. With the same reasoning, the amount of organic carbon retained in the lake is about the same quantity as the measured planktonic primary productivity. The only information on usability of the DOC+DON comes from our stream research where microbes did attach and grow when glass slides were incubated in the dark in the flowing Kuparuk River. Our educated guess, based upon the relatively high numbers of bacteria and microzooplankton in Toolik Lake, is that the DOC+DON does contribute to bacterial growth and possibly to higher trophic levels.

Our evidence for links to higher trophic levels comes from the correlation between bacterial and algal production studied in limnocorral fertilization experiment. In this experiment the chlorophyll a increased 10-20 fold, the bacterial numbers increased 4-fold, and the bacterial production increased about 8-fold. The bacterial production rates of 10^6 cells ml^{-1} d^{-1} are high for arctic lakes and are similar to temperate system rates. It was also evident that flagellate numbers and production increased in response to the increased bacterial production, and there was some evidence that grazing by flagellates in fact controlled bacterial numbers.

Certainly if there are higher numbers of flagellates, then more carbon will be transferred to zooplankton grazers. In an experiment in a limnocorral in Lake N-2, leucine-^{13}C was added weekly to the water in order to label the bacteria. By the end of the summer, the large zooplankton were quite heavily labeled with ^{13}C. This indicates that either the zooplankton consume bacteria directly or that there is a transfer of carbon from bacteria to flagellates to zooplankton.

The experiment planned for the summer of 1991 will involve additions of inorganic nutrients and of terrestrial DOC. Phytoplankton will be labelled with ^{13}C-bicarbonate, and thus the DOC from algal exudates can be distinguished from the unlabelled terrestrial DOC. The experiment will give us more information about the availability of DON and DOC to lake microbes, the importance of phytoplankton versus allochthonous DOC, and the amount of carbon transfer up the microbial food web to larger zooplankton and on to fish.

Land-water interactions

Research Needed. To achieve one of our major long-term objectives of understanding controls of water and nutrient flux at the whole watershed and regional levels, we will address four major questions:

1. What is the role of various units of landscape in determining the amount and chemistry of water flowing from land to rivers and lakes?
2. What is the specific role of the riparian zone in modifying the chemistry of water entering rivers and in determining the amount of allochthonous organic matter and light reaching the river?
3. What is the role of lakes in retaining and transforming organic matter and nutrients as they move downstream through a drainage?
4. How do the communities of rivers and lakes change in response to changes in water quantity and quality caused by various units of landscape, riparian zones and upstream lakes?

Our work on the chemistry of soil and soil water and the nitrogen and phosphorus turnover in soils gives a good starting point for expecting that different terrestrial ecosystems will yield very different quality runoff water (#1). The pilot studies on riparian and hyporheic zone effects on water chemistry need to be continued and expanded (#2). In future research, we need to focus on determining the relationships between larger landscape units (up to say 0.1 to 1 km^2) and water quality of runoff, and also the role of a series of lakes, such as is found along the inlet river to Toolik Lake, in determining river water quality (#3). From our history of experiments of nutrient fertilization of lakes and rivers, we know that lake and stream biota are very responsive to both short- and long-term changes in phosphorus and nitrogen supply. The chemical form of nutrients and carbon, as well as the amounts, can have important effects on the growth of organisms in aquatic systems. Thus we have a large amount of information on the last question (#4).

Modeling. In the future we will make modifications of our plot-based model, and link our biogeochemical model to a hierarchical GIS to scale our knowledge of ecosystem processes from experimental plots (1 m^2) to hill slopes (1 km^2), landscapes (LTER site 25 km^2), catchments (Kuparuk basin 143 km^2), regions (North Slope), and ultimately the whole Arctic.

Modifications to the Plot-based Model: First, because some of the vegetation on the tundra is phosphorus limited, we will need to incorporate phosphorus and its effects on plant growth, plant tissue allocation, and decomposition. Second, because most tundra soils are waterlogged, we will need to modify the structure to account for anaerobic metabolism in the soils and the production of methane. This is part of a need to incorporate gas fluxes into the model in order to account for losses of dissolved gases to surface waters and to accurately predict the carbon balance of the tundra. Finally, much of the data for validation, including satellite data, is seasonal data, and we will therefore need to introduce seasonality into the model. We have requested funding from both NSF and NASA to make these modifications as part of our ongoing modeling and scaling efforts.

Non-Interactive Scaling: Along with Skip Walker of the University of Colorado, we are developing a proposal to NASA to link GEM to a hierarchical GIS. The object of this research will be to scale our knowledge of biogeochimical processes acting on 1 m^2 plots to intesively mapped 1 km2 areas. The scaling will proceed in steps going from a resolution of 1 m^2 to 100 m^2, from 100 m^2 to 10^4 m^2, and finally from 10^4 m^2 to 1 km^2. We hope to learn how to model biogeochemical processes like photosynthesis, decomposition, and nutrient cycling at these succesively coarser scales. We already know that some of the process equations must change as the scale of resolution changes (Rastetter et al. 1991, O'Neill 1973) and we know several procedures for making these changes (Rastetter et al. 1991, King 1991), but we do not yet know which process equations will be most affected. We also hope to learn how much spatial heterogeneity can be incorporated in a single, aggregated model before the process equations no longer adequately represent the biogeochemical processes on the landscape.

The hierarchical GIS will contain the data needed to develop and test the scaling protocol. The data are hierarchically nested with information on vegetation and soils at resolutions ranging from very detailed maps of individual plants within 1 m^2 plots to the distribution of vegetation types in 100 m^2 plots to associations of vegetation on 10^4 m^2 plots. We have already collected much of the data needed for this hierarchical GIS for two 1 km^2 areas at the LTER site; one on the shore of Toolik Lake and one at Imnaviat Creek.

<u>Interactive Scaling</u>: We also plan to submit a proposal through the ARCSS to develop a scaling protocol for landscapes where the landscape units interact with one another through the movement of water and dissolved nutrients. The basis of this effort will again be the plot-based, GEM model and a GIS. In addition, we will need models for moving water and nutrients across the landscape. Our approach to the interactive scaling will again proceed in steps.

First we will use what we learned in the non-interactive scaling to extend our plot based model to represent relatively homogeneous landscape units on hill slopes. We will then link several of these landscape-unit models to a soil water and nutrient movement model to represent the biogeochemistry of a hill slope (Fig. 24). This hill-slope model will simulate the dependence of down-slope landscape units on the supply of water and nutrients from up-slope landscape units and the spread of disturbance associated with the movement of water and nutrients.

The hill-slope model is likely to be too complex to serve as a basis for further scaling up without some simplification. Because of the interactions among landscape units, this simplification will be far more difficult than the aggregation in the non-interactive case. Monte-Carlo simulations will be run to identify the important relationships between environmental properties (like CO_2 concentration, climate, or nutrient deposition), hill-slope characteristics (like the distribution of vegetation types or the steepness of the slope), and hill-slope responses (like water and nutrient releases to streams and lakes). From these simulations we hope to infer a simplified model structure that can be used to scale up beyond the hill-slope level. There may be several such simplified models depending upon what question is being addressed and what properties are being scaled. For example, the simplified model for water and nutrient movement from the hill slope to a stream or lake will probably not be adequate for addressing questions of C storage on the hill slope.

Once an appropriate hill-slope model has been developed, the scaling can proceed to coarser levels. For example, several hill-slope models might be used to examine the nutrient budget of a stream reach or lake (Fig. 24). Because the hill slopes do not interact with one another, an aggregated model of the hill-slope contributions of nutrients could be developed using the procedures used for the non-interactive scaling. This aggregated hill-slope model would then be linked to a biogeochemical model of the stream reach or lake to predict down-stream discharge of nutrients.

Monte-Carlo simulations could again be used to infer a simplified structure for this stream reach or lake model. This model would be linked to a channel routing model to develop a catchment or river basin model (Fig. 24). This sequence of non-interactive scaling, interactive scaling, and simplification can be repeated at various scales to develop regional models for the North Slope and ultimately for the entire Arctic.

REFERENCES

Batzli, G. O., and H. Henttonen. 1990. Demography and resource use by microtine rodents near Toolik Lake, Alaska. Arctic and Alpine Research 22:51-64.

King, A. W. 1991. Translating models across scales in the landscape. In M.G. Turner and R.H. Gardner (eds), pp.479-518, Quantitative Methods in Landscape Ecology, Springer-Verlag, New York.

Miller, M. C., G. R. Hater, P. Spatt, P. Westlake and D. Yeakel. 1986. Primary production and its control in Toolik Lake, Alaska. Arch. Hydrobiol./Suppl. 74 1:97-131.

O'Neill, R. V. 1973. Error analysis of ecological models. In D.J. Nelson (ed) Radionuclides in Ecosystems, pp.898-908. CONF-710501. NITS, Springfield, VA, USA.

Rastetter, E. B., A. W. King, B. J. Cosby, G. M. Hornberger, R. V. O'Neill, and J. E. Hobbie. In Press. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. Ecological Applications.

Shaver, G. R., and F. S. Chapin, III. 1991. Production:biomass relationships and element cycling in contrasting arctic vegetation types. Ecological Monographs 61:1-31.

FIGURE LEGENDS

Fig. 1. Location of Arctic LTER research site at Toolik Lake, Alaska.

Fig. 2. Mean length of the longest leaf in tillers of transplanted tussocks of Eriophorum vaginatum, and in untransplanted "local controls, in five reciprocal transplant gardens between Eagle Creek and Prudhoe Bay, Alaska. The location of the garden is indicated on the horizontal axis, and the populations from which the tussocks came are indicated by: solid line = "local controls"; dotted line = Eagle Creek; short dashes = No Name Creek; long dashes = Toolik Lake; single dot and dashes = Sagwon; double dots and dashes = Prudhoe Bay.

Fig. 3. Yearly mean inflorescence density relative to the long-term mean for Eriophorum vaginatum at 34 sites between Fairbanks (= Smith Lake) and Prudhoe Bay, 1980-1983. Data are given as means ± standard errors.

Fig. 4. Flowering (# inflorescences per plot) of E. vaginatum at six of the fertilized moist tundra sites, by year and treatment (C = control). All sites were fertilized in 1976, so the flowering response in 1978 represents the third year of the experiment. Although a full factorial experiment was set up in 1976 at Eagle Creek, and another one at Toolik Lake in 1978, to facilitate comparisons only the results of treatments that correspond among all sites in the 1976b series are shown. Data are given as means ± standard errors.

Fig. 5. Annual primary productivity (summer) from 1975 to 1988 in Toolik Lake plotted against the discharge of the nearby Kuparuk River.

Fig. 6. The numbers per liter of two species of zooplankton in Toolik Lake, 1976-1988.

Fig. 7. Mean daily discharge in the Kuparuk River for summers 1983-1990.

Fig. 8. Photosynthesis and respiration in the Kuparuk River. Values determined by oxygen change in enclosures of rocks from riffles in the control reach of the river.

Fig. 9. Mean density of black flies in control and fertilized reaches of the Kuparuk River for summers 1984-1990.

Fig. 10. Mean change in weight of arctic grayling in control and fertilized reaches of the Kuparuk River for summers 1986, 1988-1990.

Fig. 11. Effect of two years of experimental treatment on biomass, N mass, and P mass of Eriophorum vaginatum in a field experiment in moist tundra at Toolik Lake, Alaska. E. vaginatum is a tussock-forming sedge that is the dominant plant in this vegetation; the data presented here are the amounts of live biomass, N, and P per 32.2 cm^2 core taken through the center of 4-6 replicate tussocks in each treatment. Hatched bars represent unfertilized treatments; dotted bars represent treatments fertilized with both N and P. Ct = controls (no additional treatment); G =

fertilized and unfertilized plots contained within a greenhouse that raised average air temperatures by 5° C during the growing season; S - plots covered by shade cloth that reduced light intensity by 50 per cent. Only the three fertilizer treatments had any significant effect on biomass, N mass, or P mass, and the effects were the same with or without the greenhouse or shade treatments. Data are given as means ± standard errors.

Fig. 12. Effect of three and nine years of experimental treatment on aboveground net primary production of moist tussock tundra at Toolik Lake, Alaska. The experiment was begun in 1980, and harvested in 1983 and 1989. Treatments were the same as in Figure 11, but done on separate plots and harvested in different years; in this case the whole community response was assayed, rather than a single species. Again, the response to fertilizer was most dramatic, and this response was the same whether or not it was accompanied by increased air temperature due to the greenhouse. Data are given as means ± standard errors.

Fig. 13. Cumulative C respiration, N mineralization, and P mineralization in soils from surface (A) and subsurface (B) horizons of six arctic ecosystems during 13-week incubations at (left to right) 3, 9, and 15° C. For each panel, soils with the same letter above each group of three bars are not significantly different from each other. Note log scale for the N and P mineralization plots. Data are given as means ± standard errors.

Fig. 14. A conceptual model of carbon and nutrient interactions in terrestrial ecosystems, using C and N as an example. There are two major pools of organic matter in the ecosystem, i.e., plants and soil organic matter. Carbon fluxes into and out of these pools are indicated by solid lines, and N fluxes by dashed lines. The "bow ties" are intended to suggest linkages between the C and N fluxes.

Bow tie #1 implies that net carbon uptake by plants (NPP) is constrained by the plant's ability to take up N, and vice versa. We suggest that in many nutrient-limited ecosystems, essentially all of the plant N supply comes from mineralization of soil organic matter (including recent litter), and that N mineralization is linked to the loss of C in soil respiration (Bow tie #2). Thus, at least in a proximate sense, the overall carbon balance of such ecosystems (i.e., the difference between NPP and soil respiration) is largely determined by carbon gains associated with N uptake balanced against carbon losses associated with N mineralization.

Fig. 15. Response of planktonic primary production to nutrient fertilization in Lake N-2 durings summers 1985-1989. Also shown are the mean numbers of the snail Lymnaea in the control (open bars) and fertilized (solid bars) sections of the lake. Data are given as means ± standard errors.

Fig. 16. Distribution of sculpin in Lakes S-6 and NE-12. Burbot appearance in sculpin traps indicates a shift in their distribution from deep water to nearshore zones after lake trout removal.

Fig. 17. Response of the Kuparuk River biota to the addition of phosphorus and to possible changes in predators. See text for explanation.

Fig. 18. Chlorophyll concentration on riffle rocks of the Kuparuk in the control and fertilized (at 0 km in 1983-84) reaches of the river.

Fig. 19. Ecosystem sites along a toposequence leading down to an arctic river.

Fig. 20. Concentrations of N and P in lysimeter water at distances (m) upstream (negative) and downstream (positive) from the nutrient dripper on the Kuparuk River, 1989. When there are a, b, and c samples at a given river distance, then the samples were collected at far (about 15 m), mid (about 6 m), and near (about 1 m) distances from the river.

Fig. 21. The delta ^{15}N values for particulate organic matter (POM, mostly phytoplankton) and for three genera of zooplankton in the control and fertilized sides of Lake N-2. The ^{15}N was added continuously as trace amounts of NH_4Cl starting on 1 July 1988.

Fig. 22. Schematic diagram of a general model of carbon and nitrogen cycles within terrestrial ecosystems.

Fig. 23. Modeled plant and soil stocks of carbon and nitrogen in tundra (upper graph) and northern hardwood forest (lower graph) after 50 years of exposure to a doubling of CO_2 concentration, a 5°C increase in temperature, a combined CO_2 and temperature increase, and a 0.1 g N m^{-2} mo^{-1} increase in nitrogen deposition.

Fig. 24. Conceptual plan of the hierarchical partitioning of tundra on the North Slope of Alaska. The sequence of larger and larger partitions (panels #1 - #4) is designed to link process studies on small plots with landscape units and finally with regional scale predictions of biogeochemical interactions, export of nutrients, or responses to disturbance or climatic change. For example, landscape units (#1) of different vegetation or soil type make up a hill slope, and several hill slopes are grouped to define a river reach (#2) of a larger drainage basin (#3). Levels in the hierarchy alternate between units that interact strongly with one another, such as landscape units on a hill slope or stream reaches within a drainage (#1 and 3), and units that act independently of one another, such as parallel hill slopes feeding the same river reach or parallel drainages on the whole North Slope (#2 and 4).

Fig. 25. Diagram of the interactions of arctic communities and their biogeochemical cylces with global climate change.

FIGURE 1

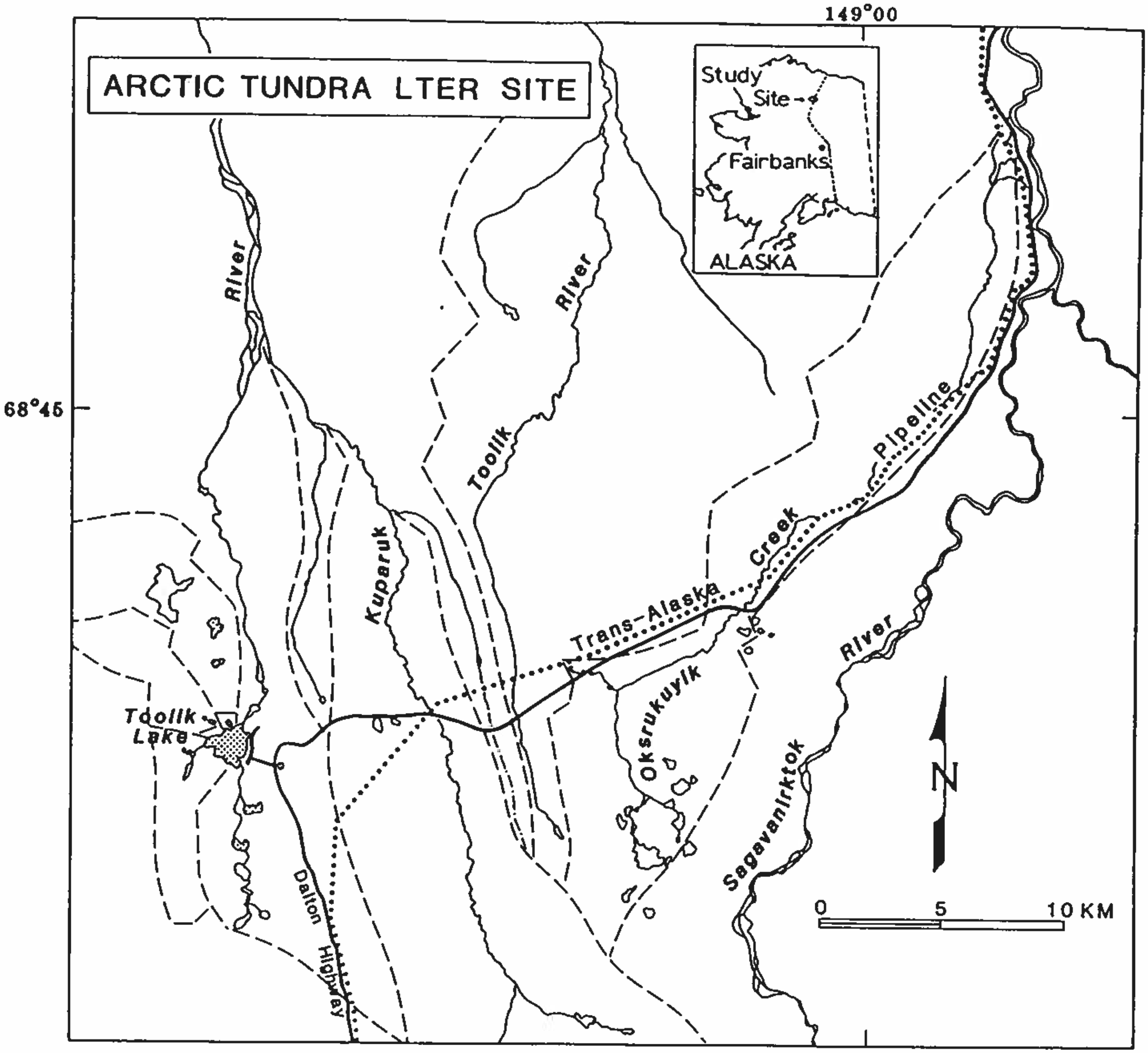

ARCTIC TUNDRA LTER SITE
149°00
68°45
Study Site
Fairbanks
ALASKA
River
Toolik River
Kuparuk
Toolik Lake
Trans-Alaska Pipeline
Creek
Oksrukuyik
Sagavanirktok River
Dalton Highway
N
0
5
10 KM

FIGURE 2

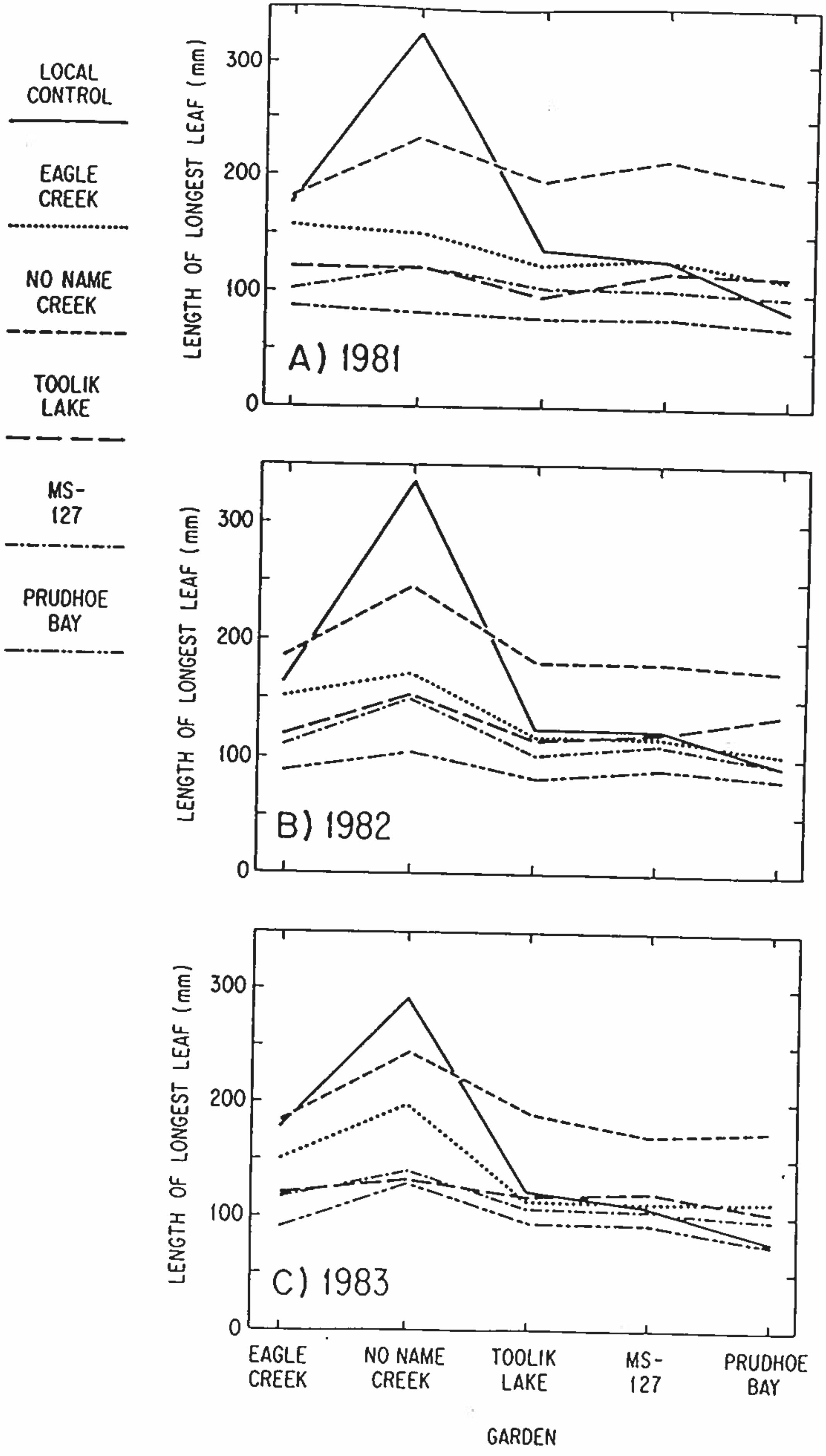

LOCAL CONTROL
EAGLE CREEK
NO NAME CREEK
TOOLIK LAKE
MS-127
PRUDHOE BAY
LENGTH OF LONGEST LEAF (mm)
0
100
200
300
A) 1981
B) 1982
C) 1983
EAGLE CREEK
NO NAME CREEK
TOOLIK LAKE
MS-127
PRUDHOE BAY
GARDEN

FIGURE 3

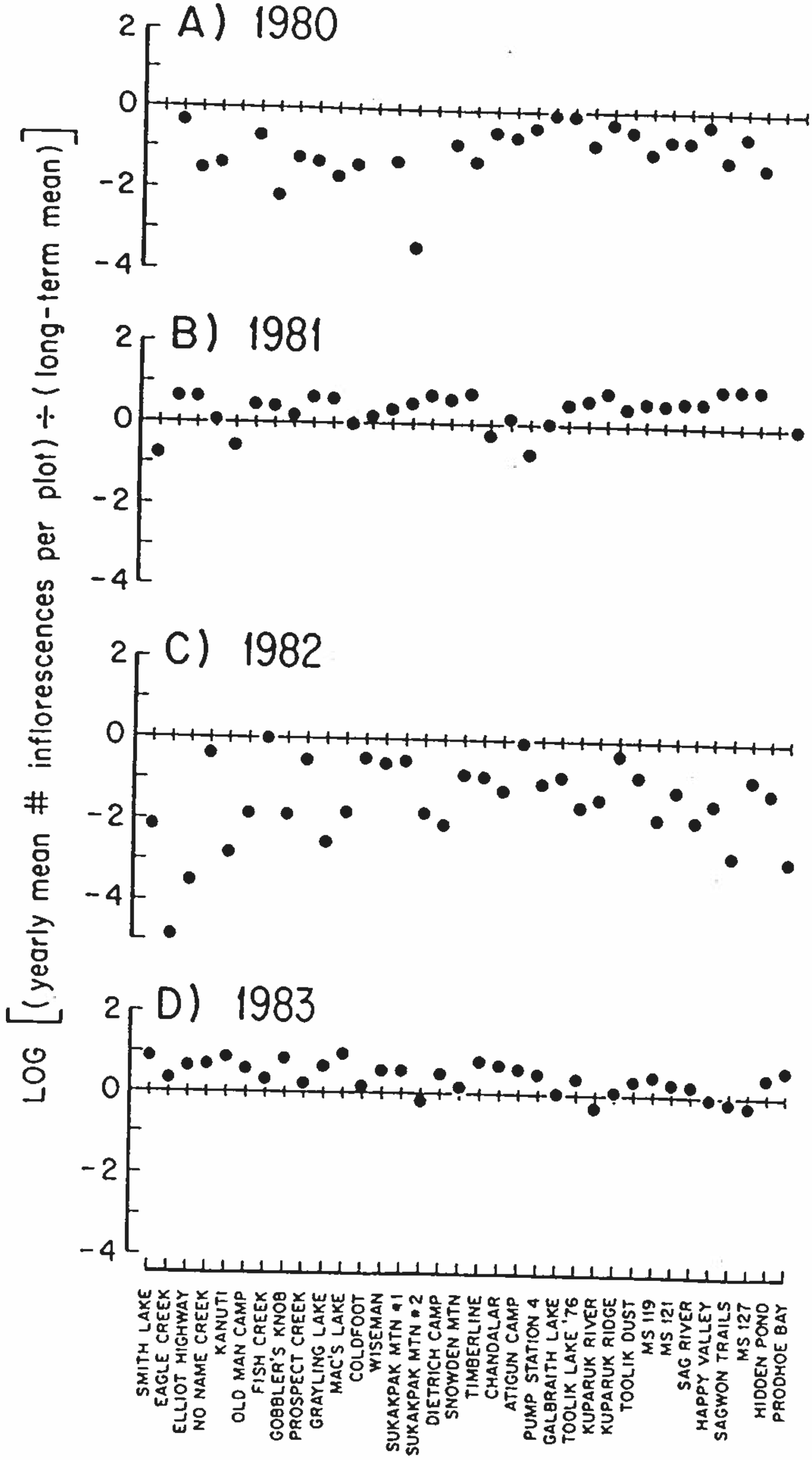
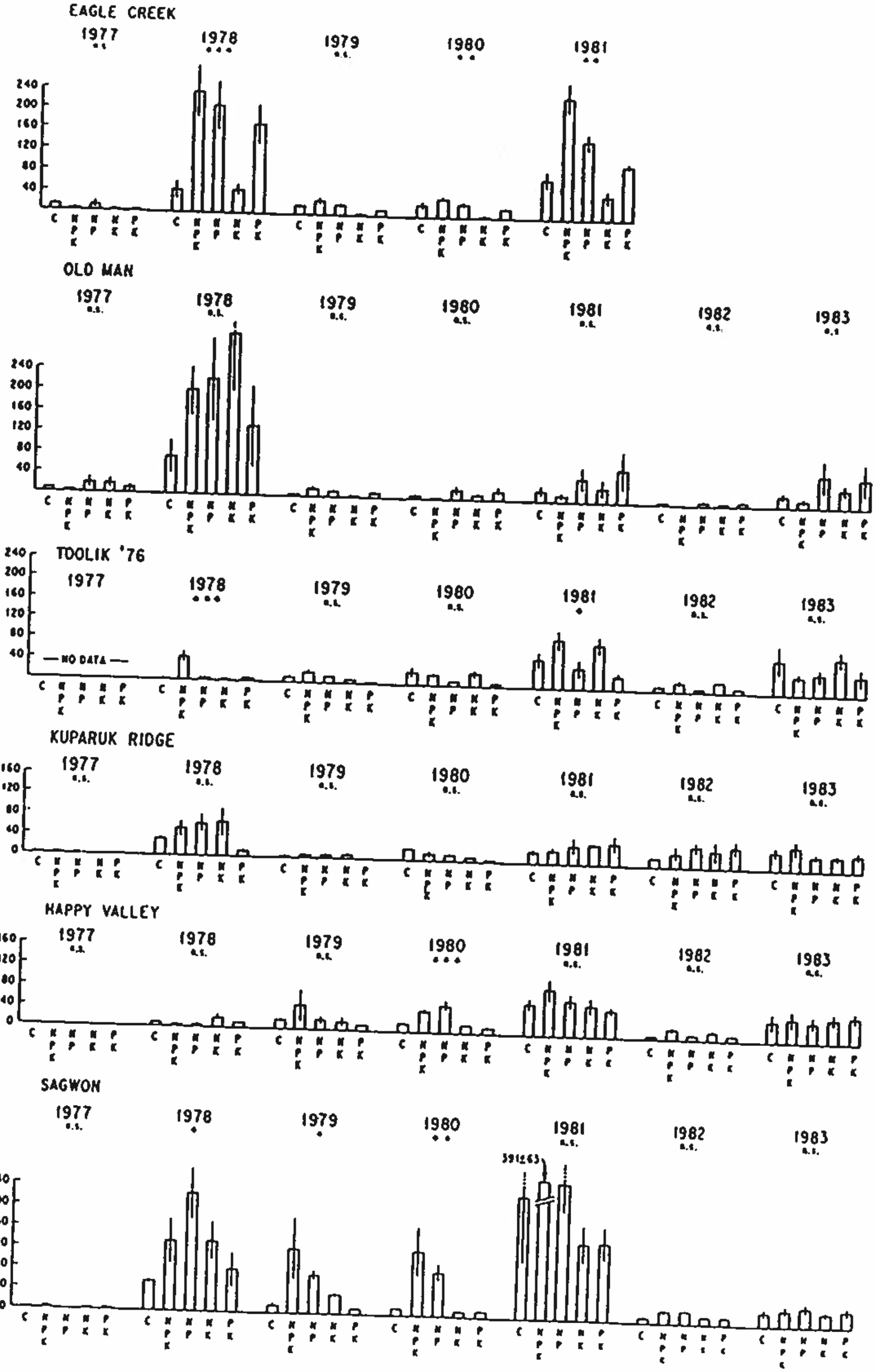
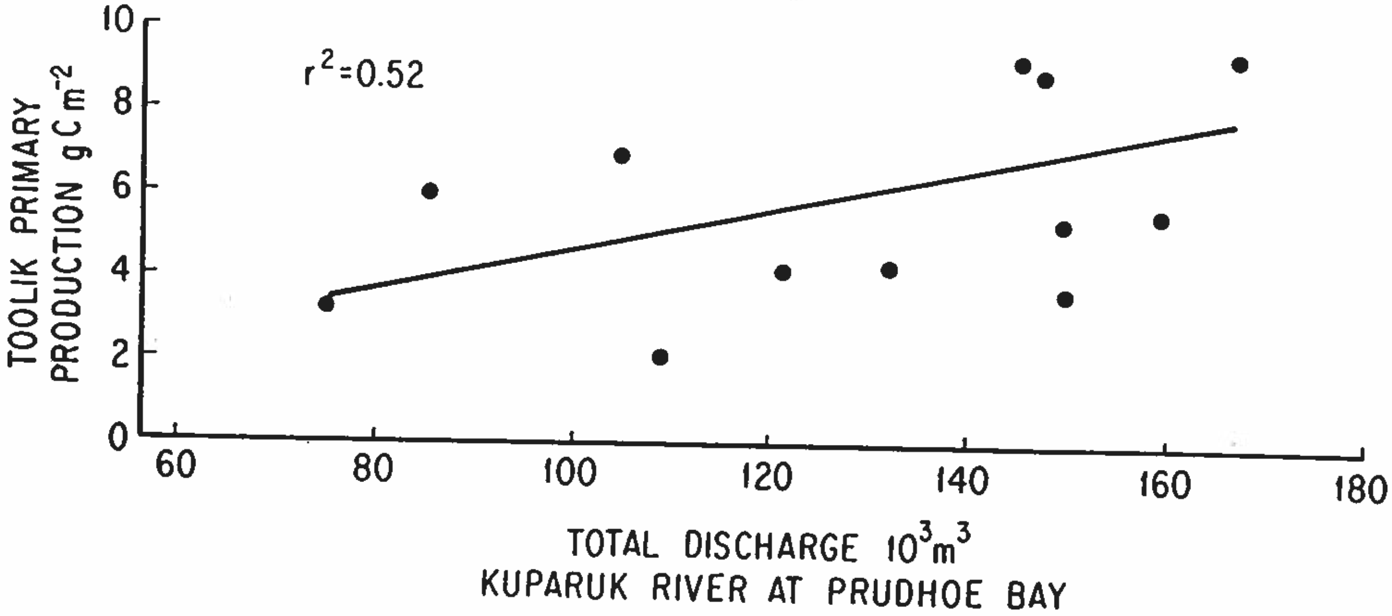

A) 1980
B) 1981
C) 1982
D) 1983
LOG [(yearly mean # inflorescences per plot) ÷ (long-term mean)]
2
0
-2
-4
SMITH LAKE
EAGLE CREEK
ELLIOT HIGHWAY
NO NAME CREEK
KANUTI
OLD MAN CAMP
FISH CREEK
GOBBLER'S KNOB
PROSPECT CREEK
GRAYLING LAKE
MAC'S LAKE
COLDFOOT
WISEMAN
SUKAKPAK MTN #1
SUKAKPAK MTN #2
DIETRICH CAMP
SNOWDEN MTN
TIMBERLINE
CHANDALAR
ATIGUN CAMP
PUMP STATION 4
GALBRAITH LAKE
TOOLIK LAKE '76
KUPARUK RIVER
KUPARUK RIDGE
TOOLIK DUST
MS 119
MS 121
SAG RIVER
HAPPY VALLEY
SAGWON TRAILS
MS 127
HIDDEN POND
PRODHOE BAY

FIGURE 4



EAGLE CREEK
1977 n.s.
1978 ***
1979 n.s.
1980 **
1981 **
OLD MAN
1977 n.s.
1978 n.s.
1979 n.s.
1980 n.s.
1981 n.s.
1982 n.s.
1983 n.s.
TOOLIK '76
1977
— NO DATA —
1978 ***
1979 n.s.
1980 n.s.
1981 *
1982 n.s.
1983 n.s.
KUPARUK RIDGE
1977 n.s.
1978 n.s.
1979 n.s.
1980 n.s.
1981 n.s.
1982 n.s.
1983 n.s.
HAPPY VALLEY
1977 n.s.
1978 n.s.
1979 n.s.
1980 ***
1981 n.s.
1982 n.s.
1983 n.s.
SAGWON
1977 n.s.
1978 *
1979 *
1980 **
1981 n.s.
1982 n.s.
1983 n.s.
391±63
0
40
80
120
160
200
240
C
NPK
NP
NK
PK

FIGURE 5



r²=0.52
TOOLIK PRIMARY PRODUCTION g C m⁻²
0
2
4
6
8
10
60
80
100
120
140
160
180
TOTAL DISCHARGE 10³m³
KUPARUK RIVER AT PRUDHOE BAY

FIGURE 6

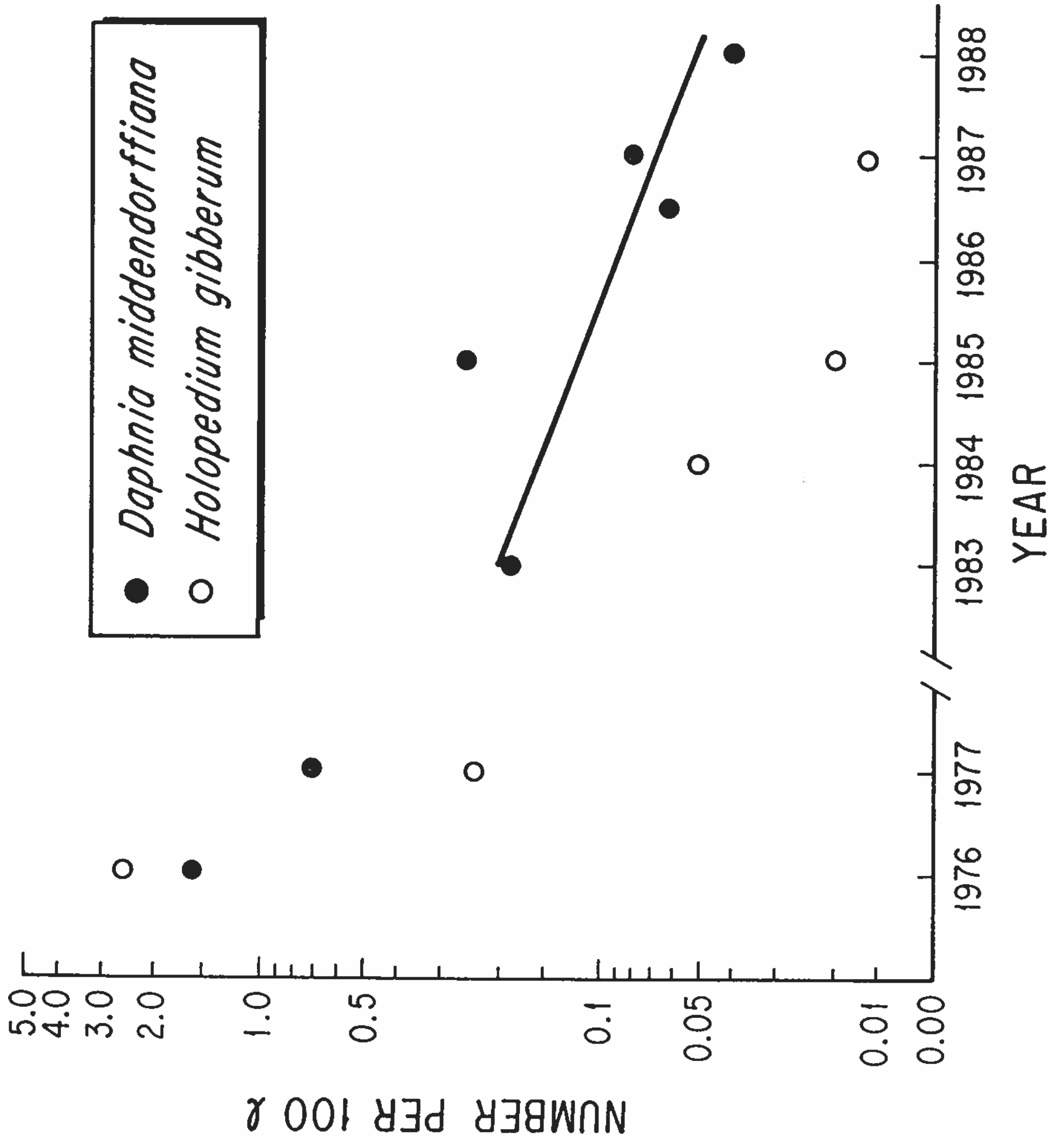

● Daphnia middendorffiana
○ Holopedium gibberum
NUMBER PER 100 ℓ
5.0
4.0
3.0
2.0
1.0
0.5
0.1
0.05
0.01
0.00
YEAR
1976
1977
1983
1984
1985
1986
1987
1988

FIGURE 7

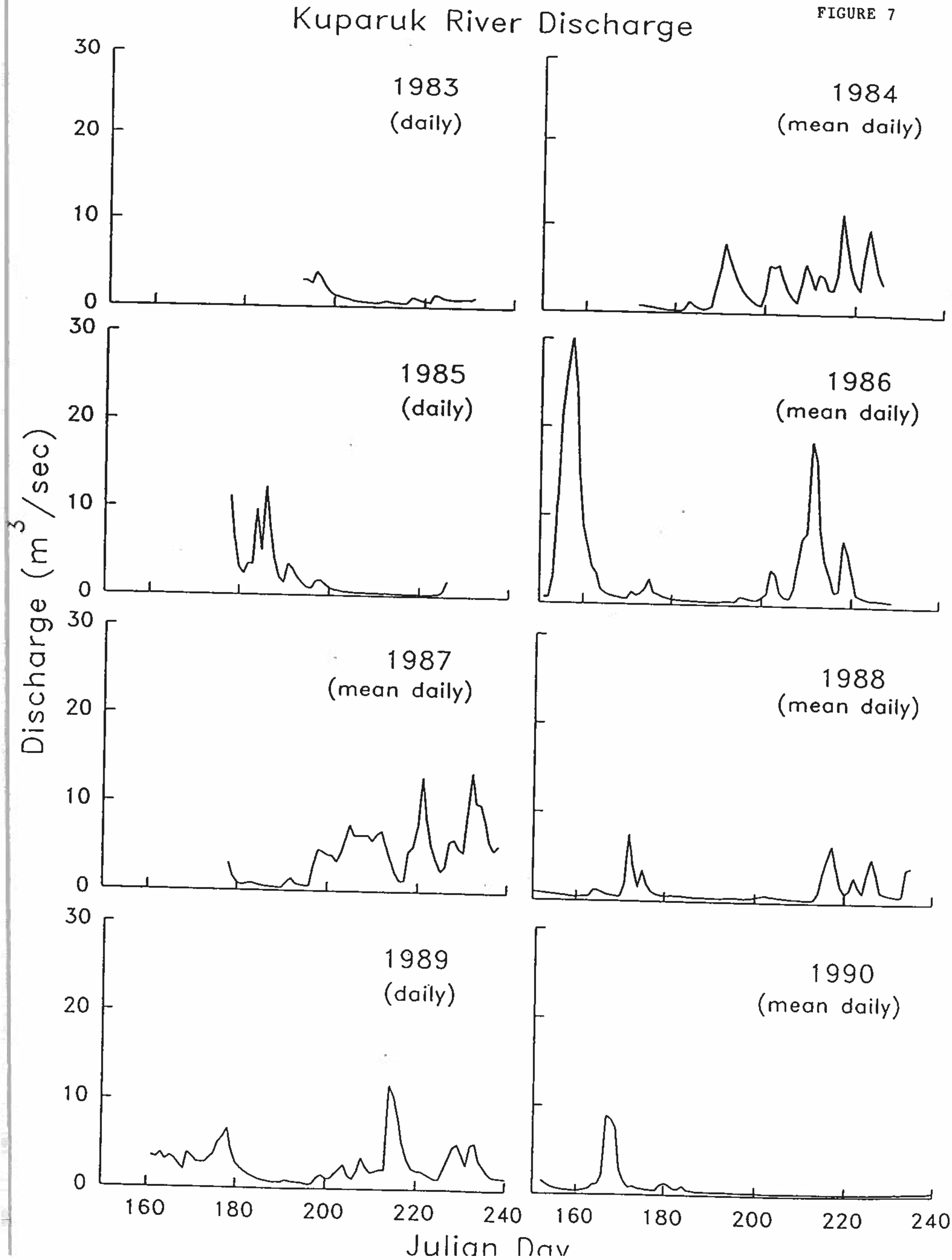
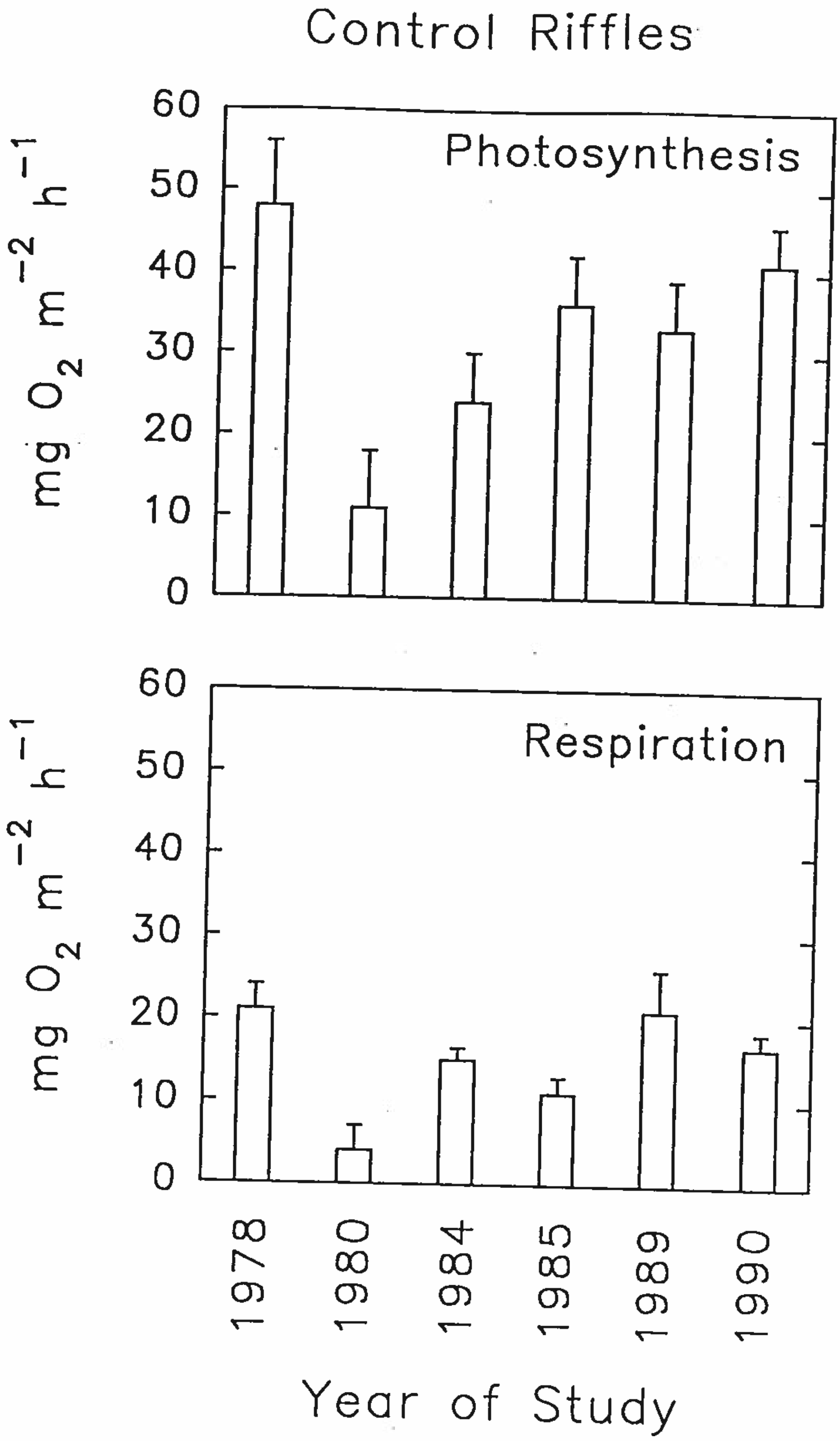

Kuparuk River Discharge
1983
(daily)
1984
(mean daily)
1985
(daily)
1986
(mean daily)
1987
(mean daily)
1988
(mean daily)
1989
(daily)
1990
(mean daily)
Discharge (m^3/sec)
0
10
20
30
160
180
200
220
240
Julian Day

FIGURE 8



Control Riffles
Photosynthesis
Respiration
mg O_2 m^{-2} h^{-1}
60
50
40
30
20
10
0
1978
1980
1984
1985
1989
1990
Year of Study

FIGURE 9

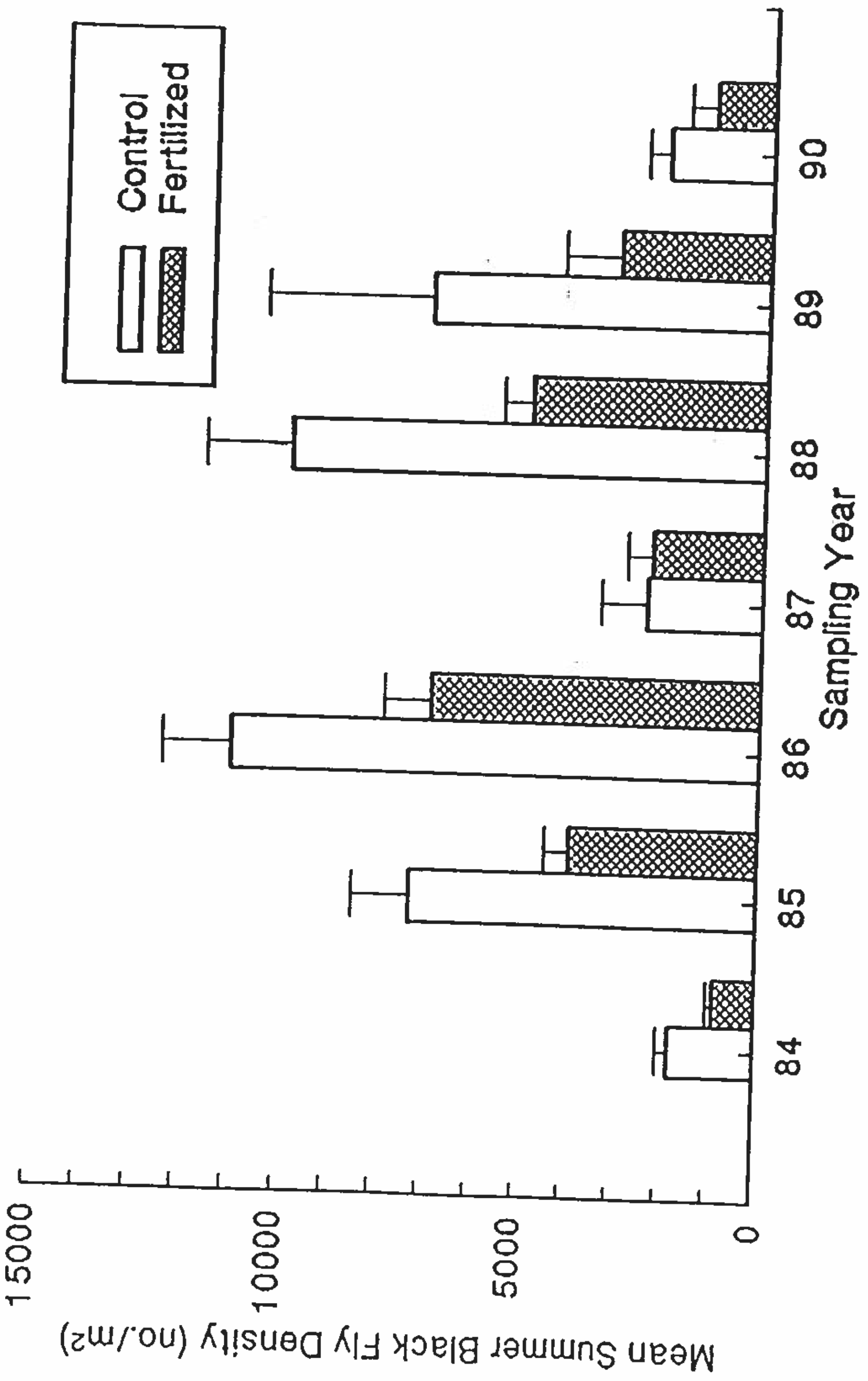
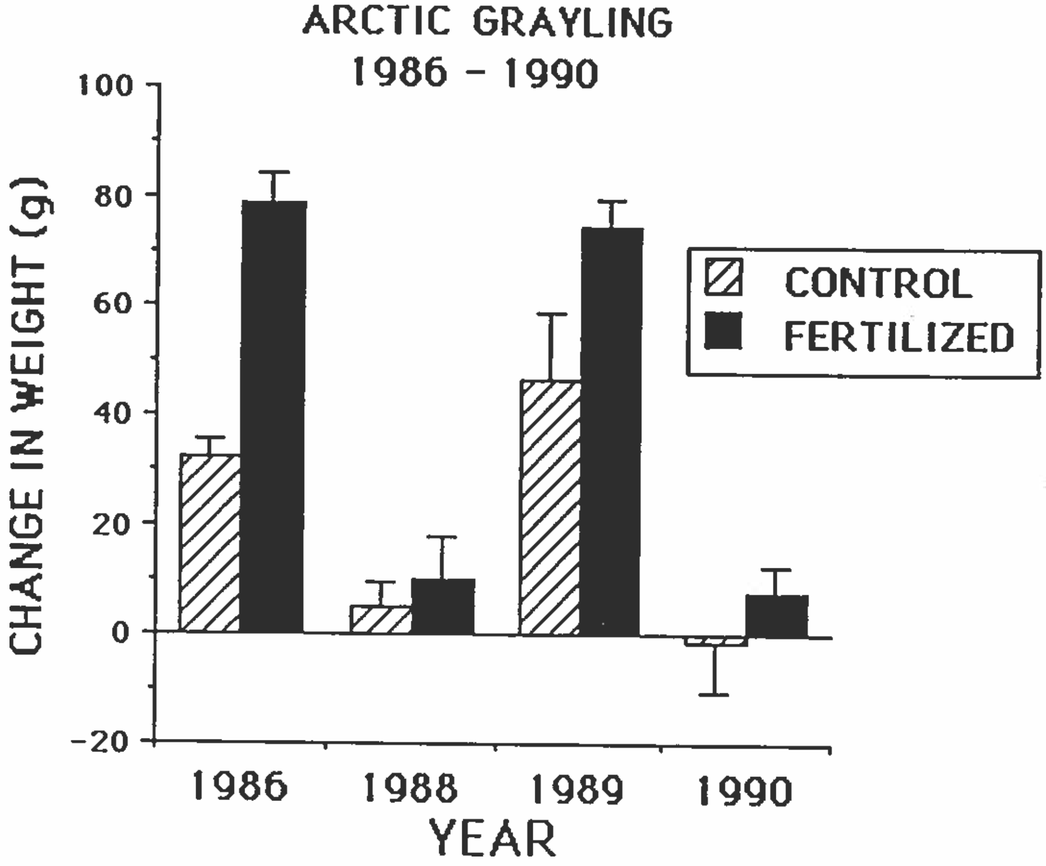

Control
Fertilized
Mean Summer Black Fly Density (no./m2)
15000
10000
5000
0
84
85
86
87
88
89
90
Sampling Year

FIGURE 10



ARCTIC GRAYLING
1986 - 1990
CHANGE IN WEIGHT (g)
100
80
60
40
20
0
-20
▨ CONTROL
■ FERTILIZED
1986
1988
1989
1990
YEAR

FIGURE 11

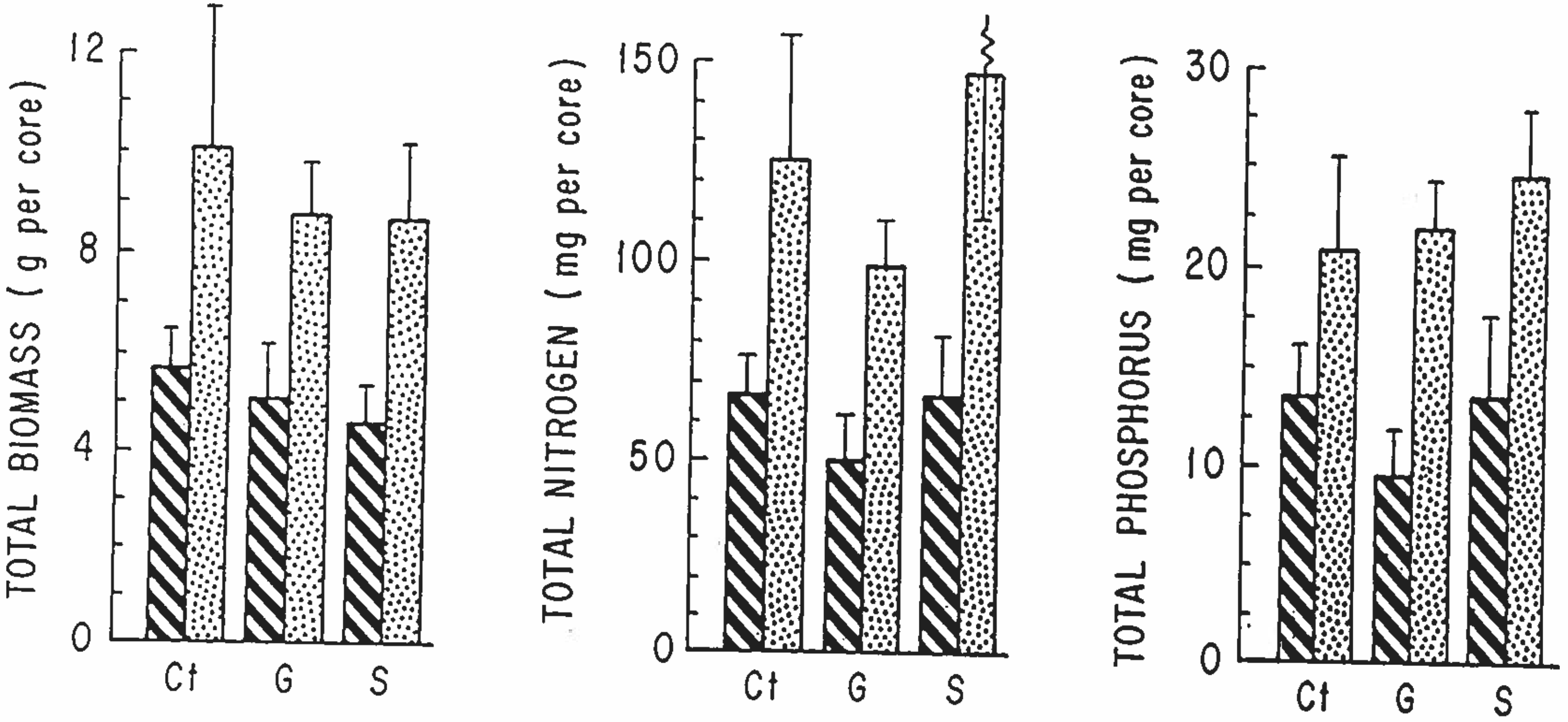
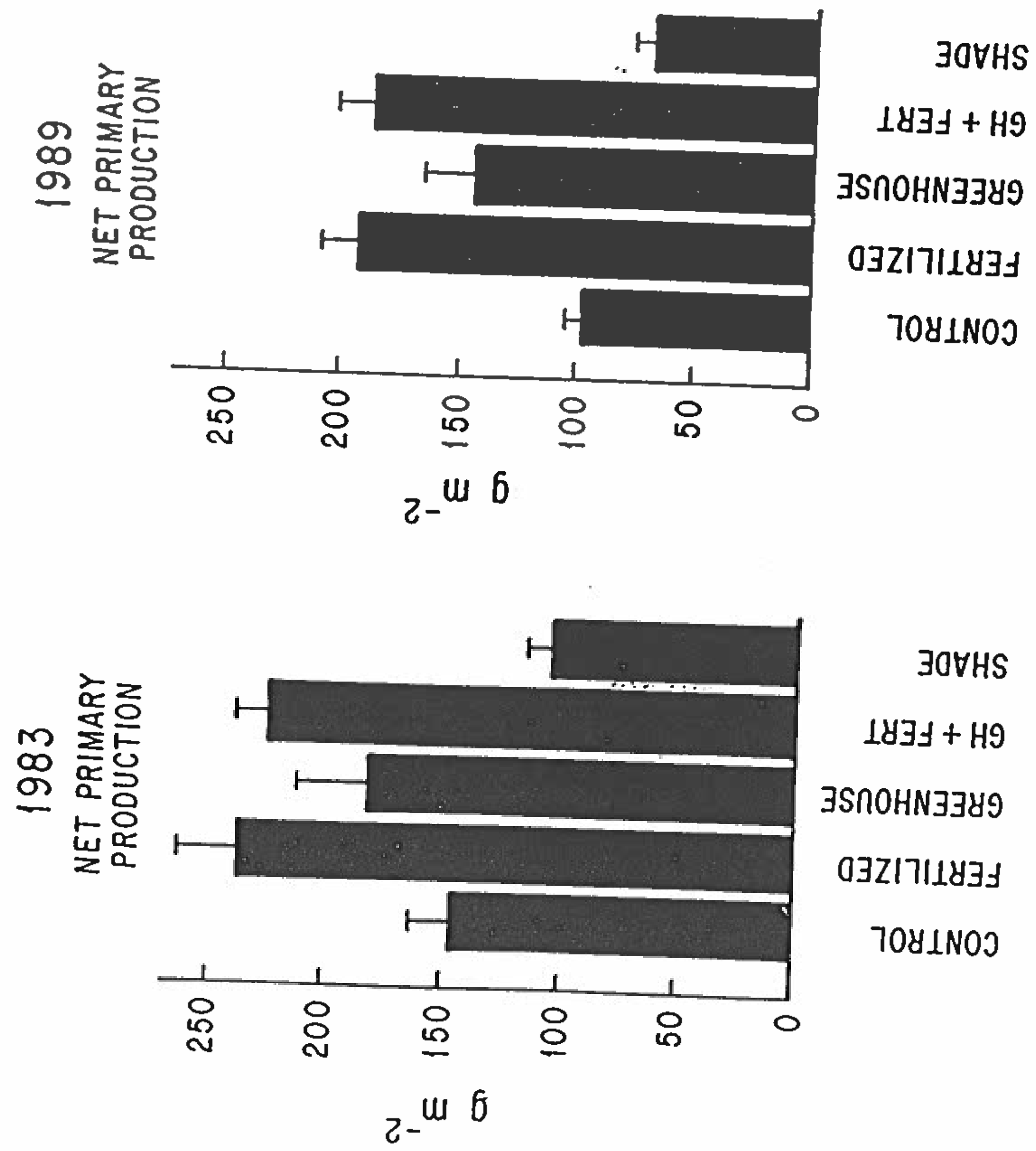

TOTAL BIOMASS (g per core)
0
4
8
12
Ct
G
S
TOTAL NITROGEN (mg per core)
0
50
100
150
Ct
G
S
TOTAL PHOSPHORUS (mg per core)
0
10
20
30
Ct
G
S

FIGURE 12


1989
NET PRIMARY PRODUCTION
1983
NET PRIMARY PRODUCTION
g m^-2
0
50
100
150
200
250
CONTROL
FERTILIZED
GREENHOUSE
GH + FERT
SHADE

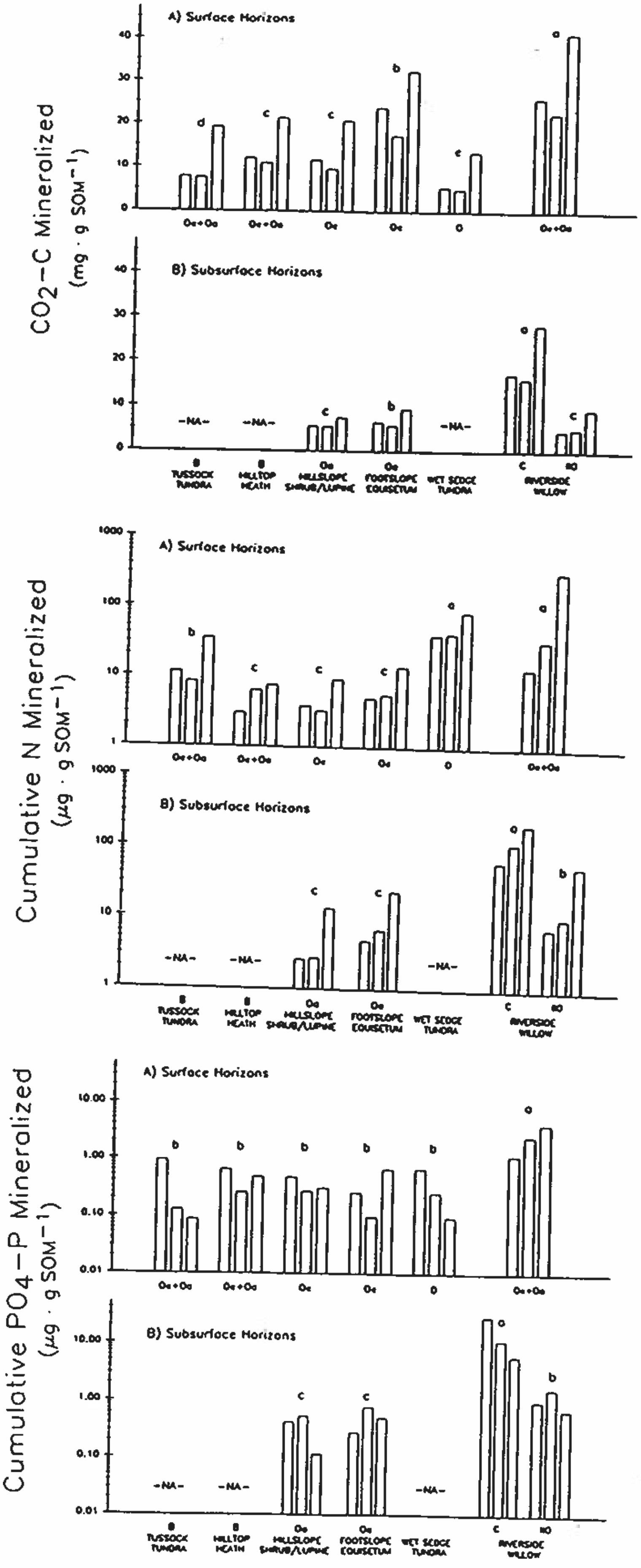

CO2−C Mineralized (mg · g SOM−1)
A) Surface Horizons
0
10
20
30
40
d
c
c
b
e
a
Oe+Oa
Oe+Oa
Oe
Oe
O
Oe+Oa
B) Subsurface Horizons
0
10
20
30
40
−NA−
−NA−
c
b
−NA−
a
c
B
TUSSOCK TUNDRA
B
HILLTOP HEATH
Oa
HILLSLOPE SHRUB/LUPINE
Oa
FOOTSLOPE EQUISETUM
WET SEDGE TUNDRA
C
80
RIVERSIDE WILLOW
Cumulative N Mineralized (μg · g SOM−1)
A) Surface Horizons
1
10
100
1000
b
c
c
c
a
a
Oe+Oa
Oe+Oa
Oe
Oe
O
Oe+Oa
B) Subsurface Horizons
1
10
100
1000
−NA−
−NA−
c
c
−NA−
a
b
B
TUSSOCK TUNDRA
B
HILLTOP HEATH
Oa
HILLSLOPE SHRUB/LUPINE
Oa
FOOTSLOPE EQUISETUM
WET SEDGE TUNDRA
C
80
RIVERSIDE WILLOW
Cumulative PO4−P Mineralized (μg · g SOM−1)
A) Surface Horizons
0.01
0.10
1.00
10.00
b
b
b
b
b
a
Oe+Oa
Oe+Oa
Oe
Oe
O
Oe+Oa
B) Subsurface Horizons
0.01
0.10
1.00
10.00
−NA−
−NA−
c
c
−NA−
a
b
B
TUSSOCK TUNDRA
B
HILLTOP HEATH
Oa
HILLSLOPE SHRUB/LUPINE
Oa
FOOTSLOPE EQUISETUM
WET SEDGE TUNDRA
C
80
RIVERSIDE WILLOW

FIGURE 14

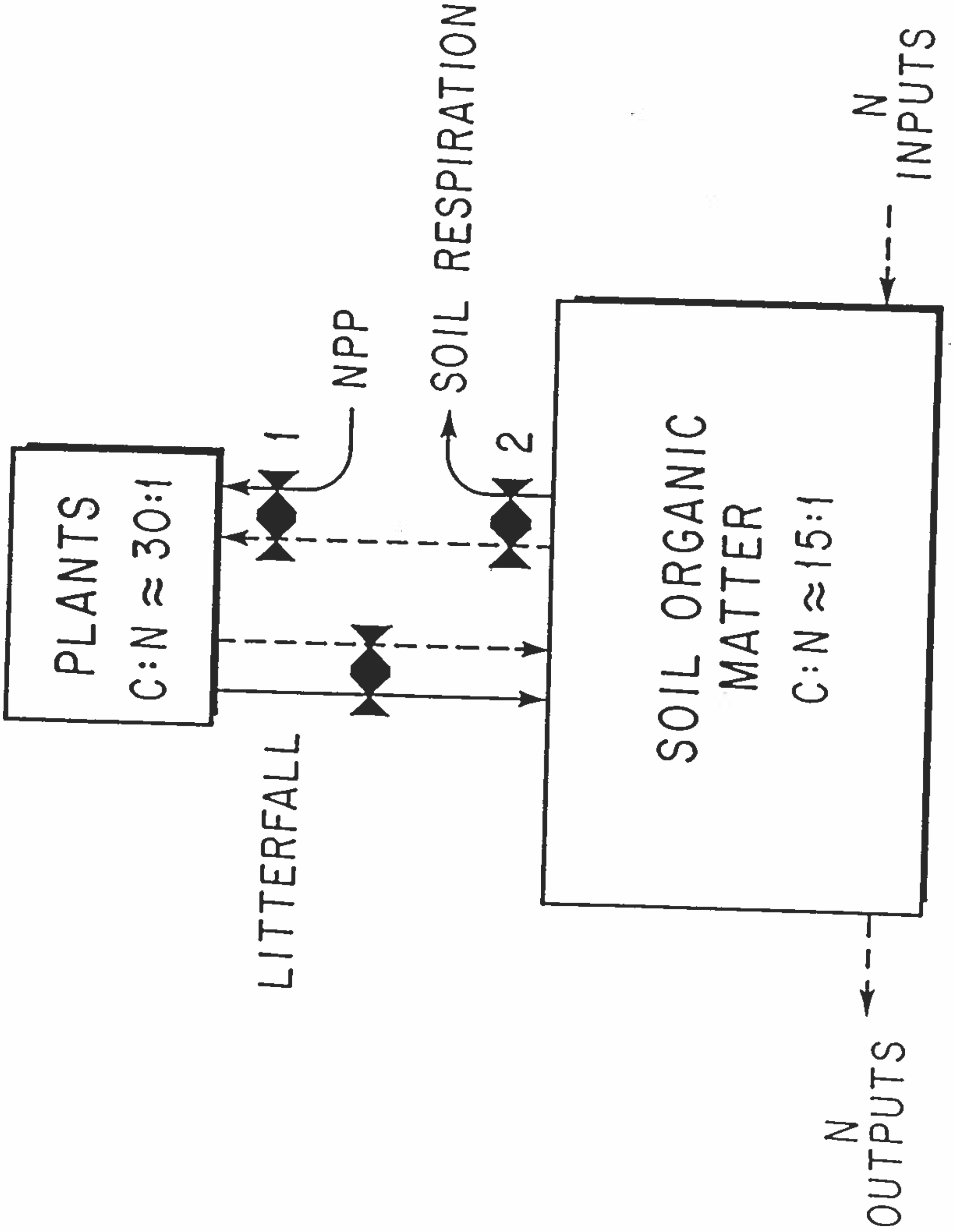
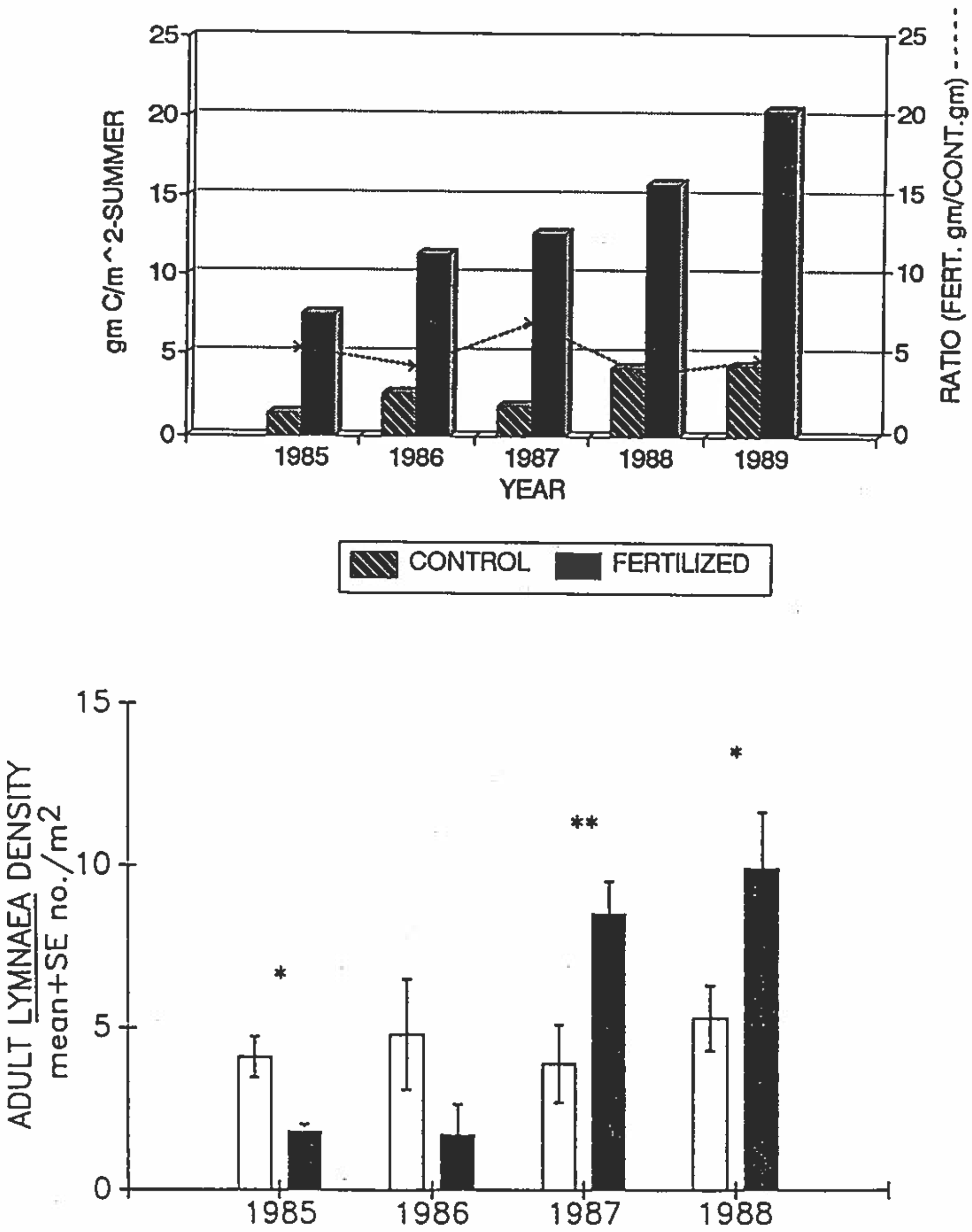

PLANTS
C:N ≈ 30:1
NPP
1
SOIL RESPIRATION
2
LITTERFALL
SOIL ORGANIC MATTER
C:N ≈ 15:1
N INPUTS
N OUTPUTS

FIGURE 15



CUMULATIVE SUMMER SESTONIC PRODUCTION
N-2, 45 DAYS OF FERTILIZATION, 1985-89

FIGURE 16

Experimental Lakes

		Percent Distribution		
LT		1988	1989	1990
Introduction: S6	ave. rock	25	13	
	interface	36	42	
	sediment	39	45	
LT				
Removal: NE12	ave. rock	28	28	48
	interface	27	43	29
	sediment	45	29	23
# of burbot in sculpin traps		0	10	9

BIOLOGICAL RESPONSES TO PHOSPHORUS ADDITION

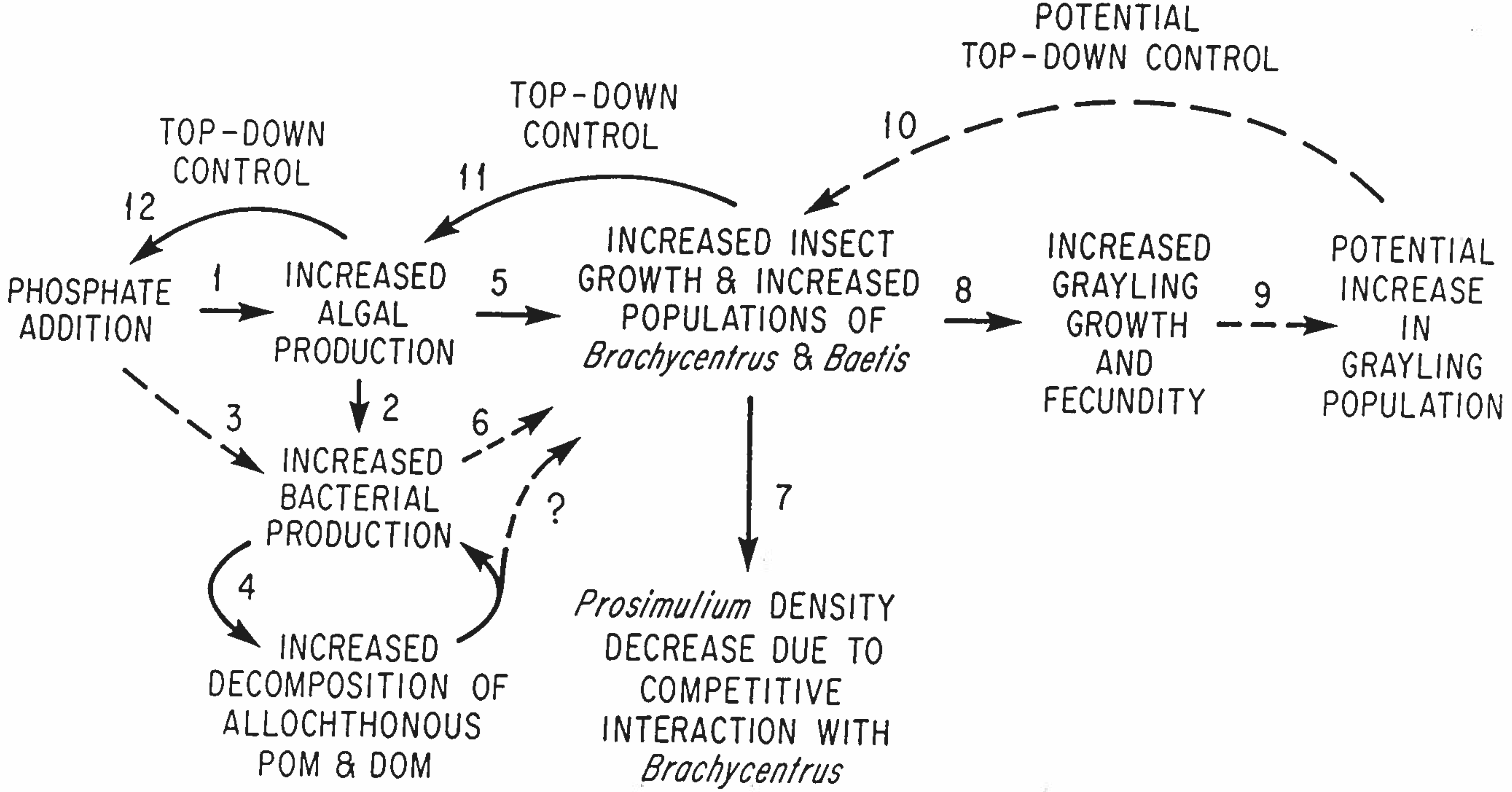
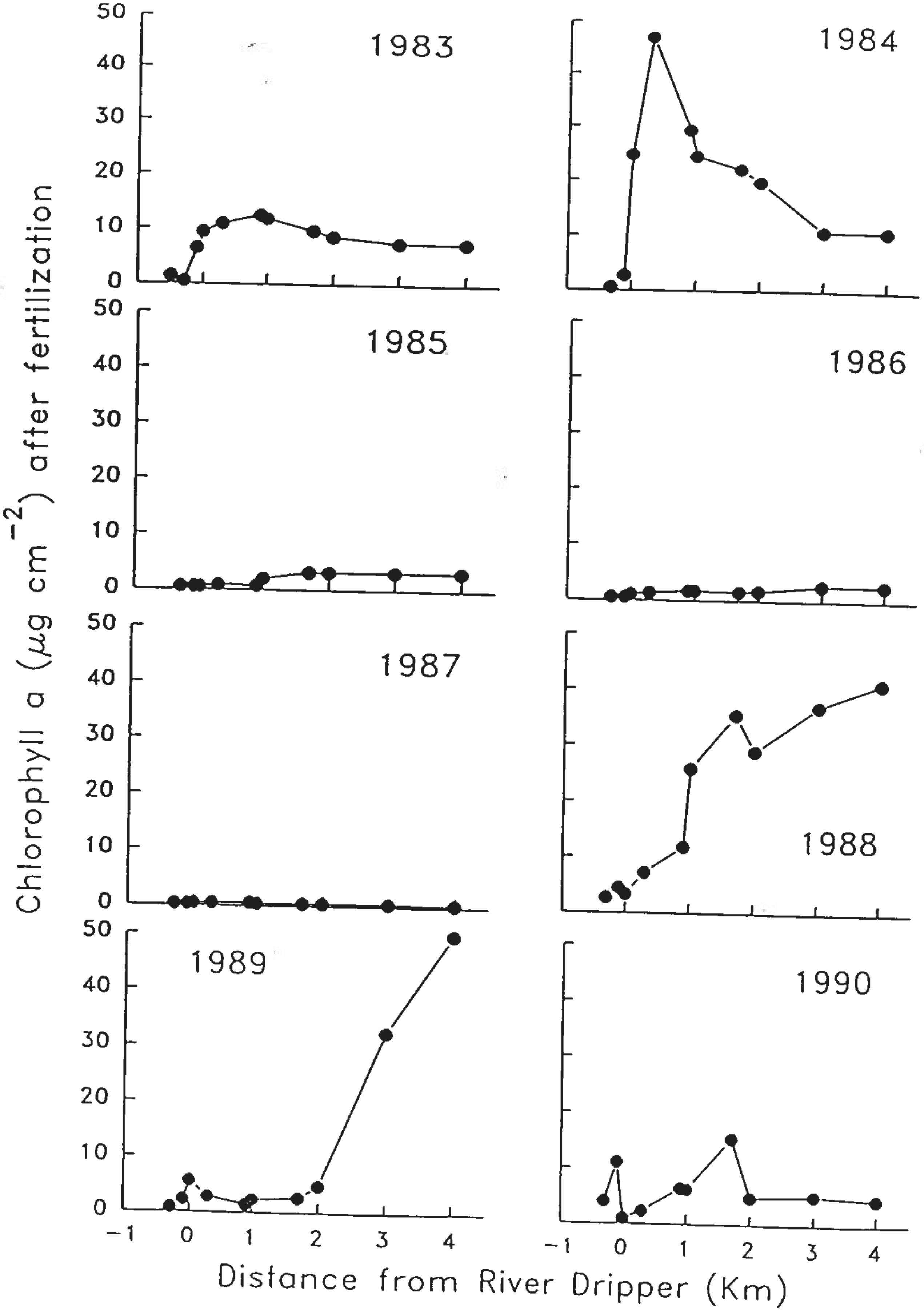


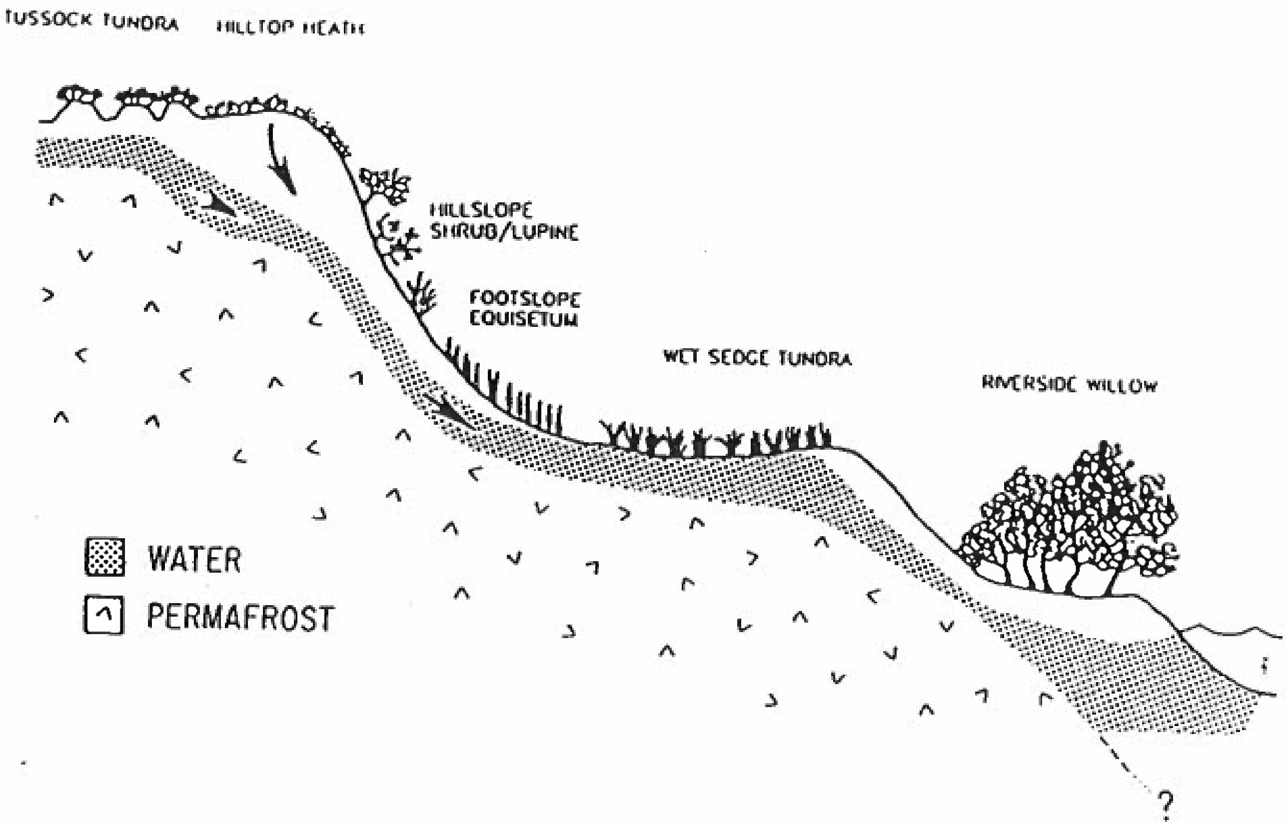
FIGURE 17

FIGURE 18



1983
1984
1985
1986
1987
1988
1989
1990
50
40
30
20
10
0
-1
0
1
2
3
4
Chlorophyll a (μg cm⁻²) after fertilization
Distance from River Dripper (Km)

FIGURE 19



TUSSOCK TUNDRA
HILLTOP HEATH
HILLSLOPE SHRUB/LUPINE
FOOTSLOPE EQUISETUM
WET SEDGE TUNDRA
RIVERSIDE WILLOW
WATER
PERMAFROST
?

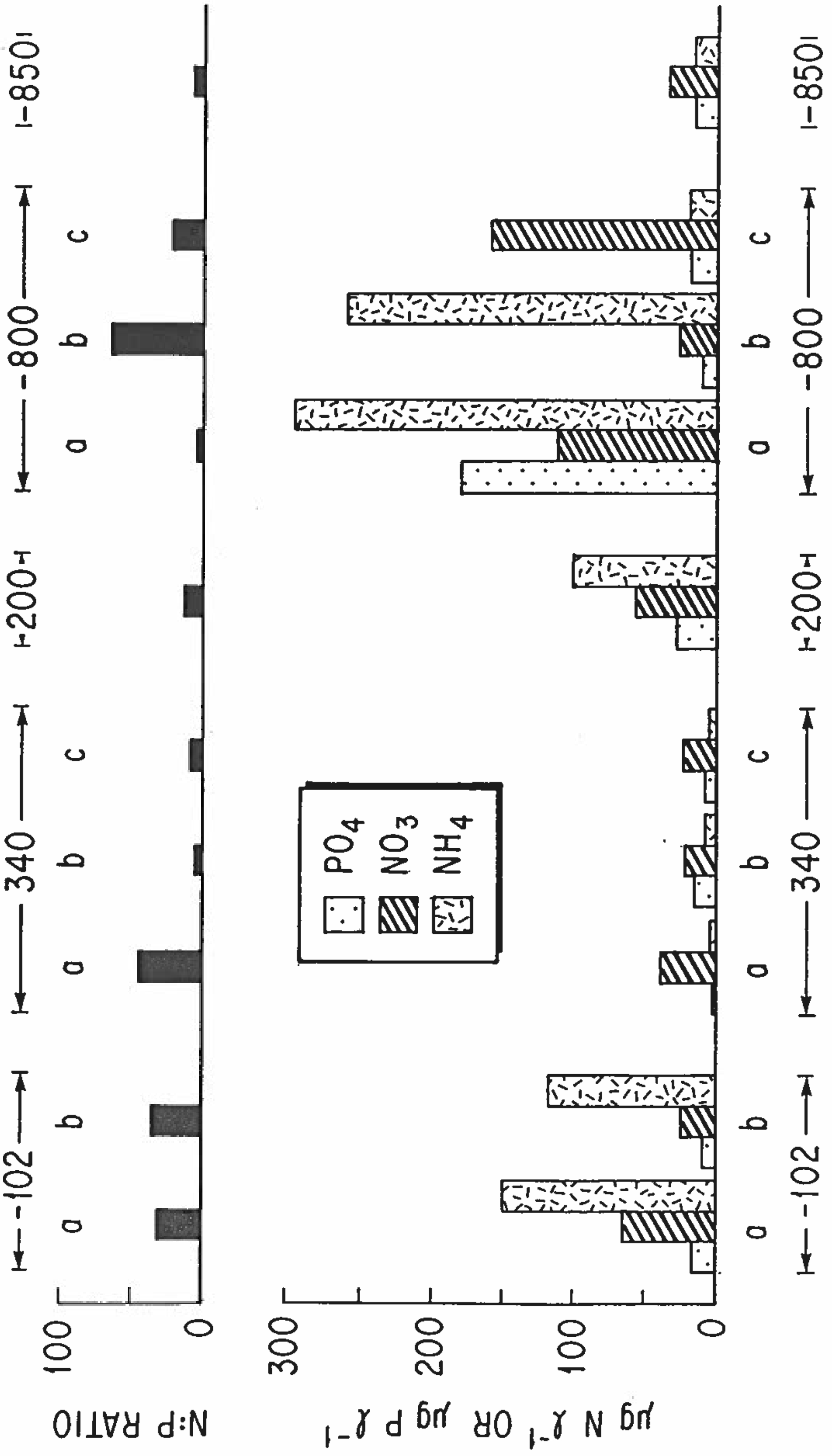
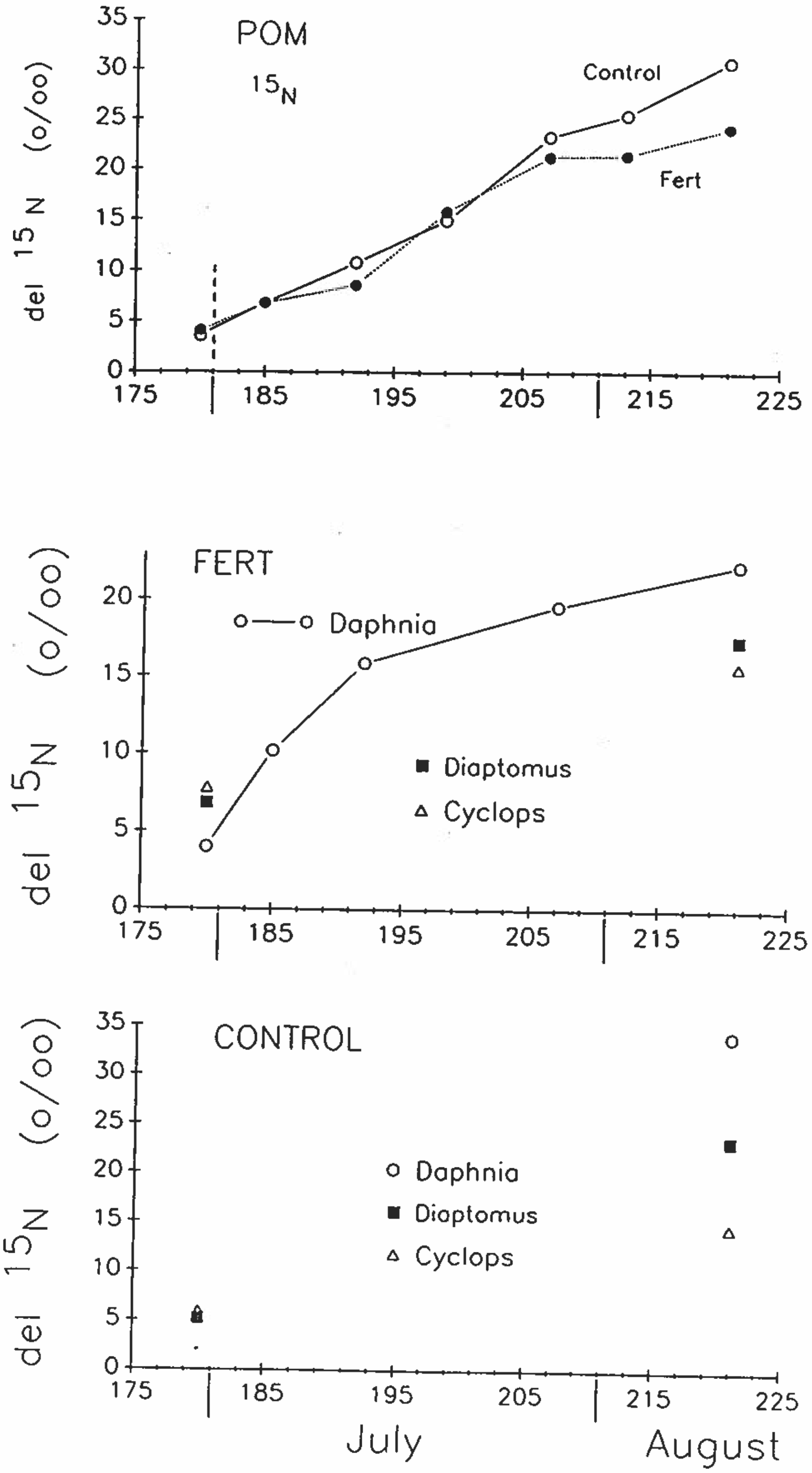

N:P RATIO
100
0
µg N ℓ⁻¹ OR µg P ℓ⁻¹
300
200
100
0
-102
a
b
340
a
b
c
-200
-800
a
b
c
-850
PO4
NO3
NH4

FIGURE 21



POM
15N
Control
Fert
del 15N (o/oo)
35
30
25
20
15
10
5
0
175
185
195
205
215
225
FERT
Daphnia
Diaptomus
Cyclops
del 15N (o/oo)
20
15
10
5
0
175
185
195
205
215
225
CONTROL
Daphnia
Diaptomus
Cyclops
del 15N (o/oo)
35
30
25
20
15
10
5
0
175
185
195
205
215
225
July
August

FIGURE 22

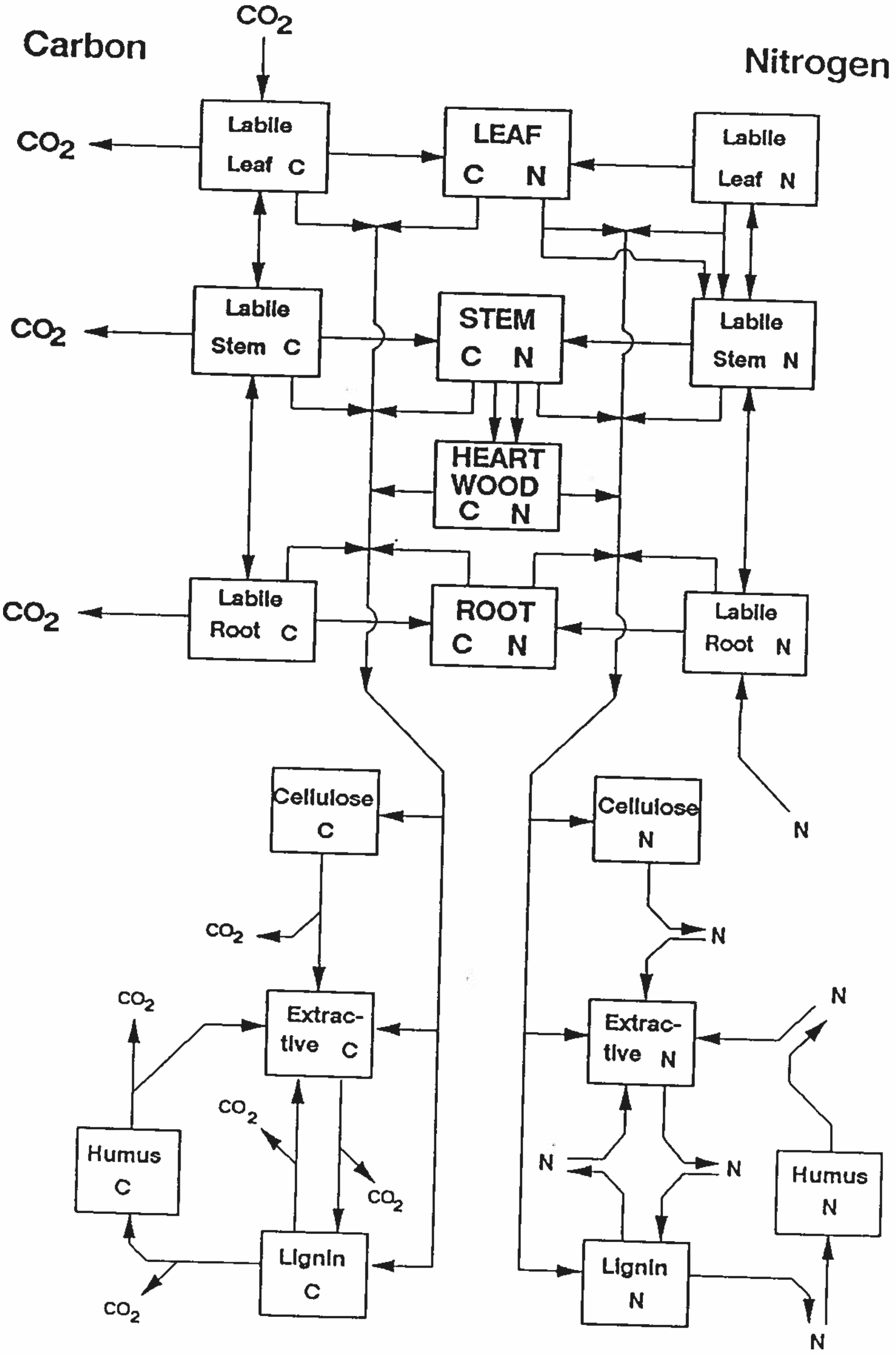
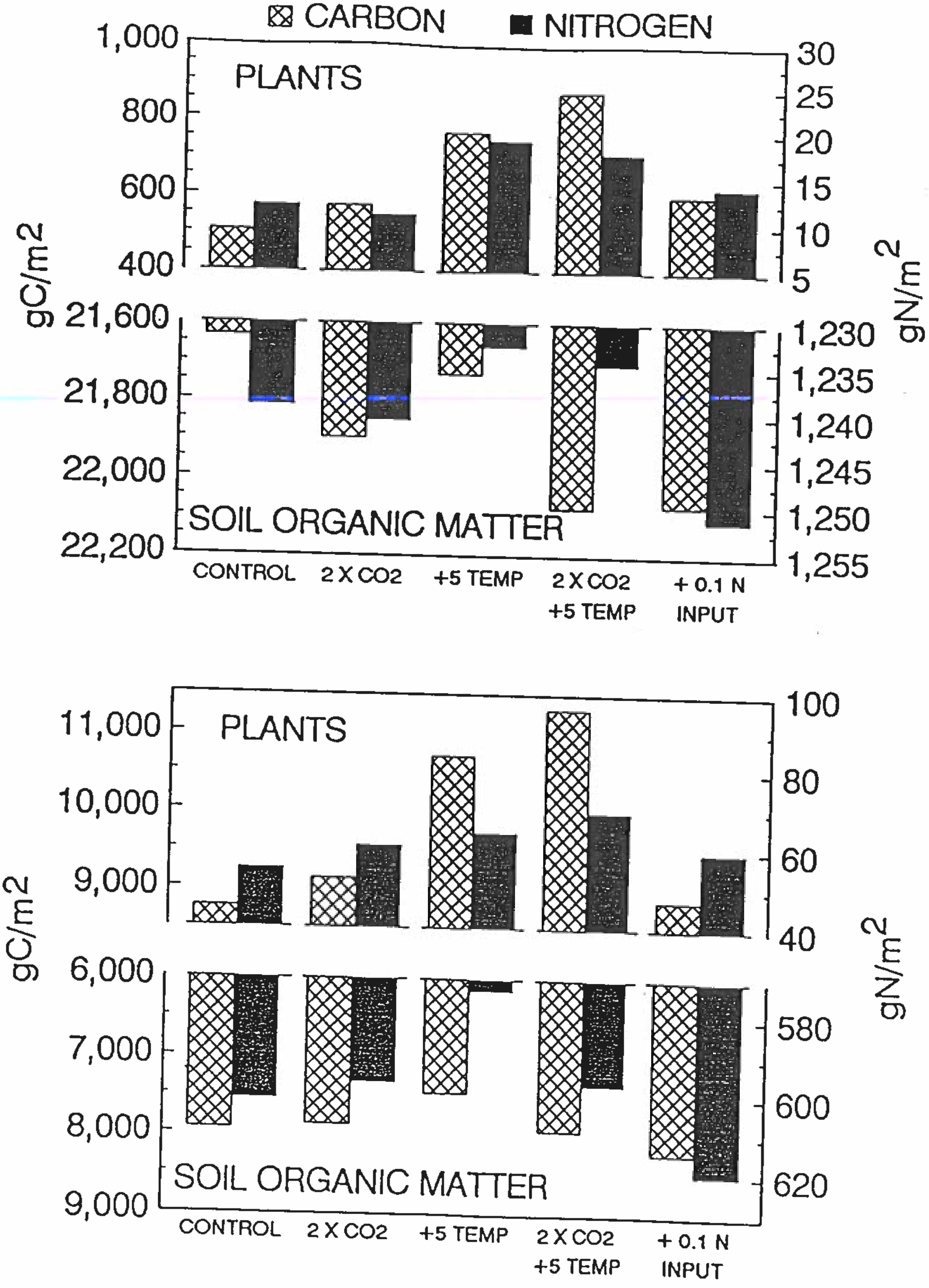

Carbon
CO2
Nitrogen
CO2
Labile Leaf C
LEAF C N
Labile Leaf N
CO2
Labile Stem C
STEM C N
Labile Stem N
HEART WOOD C N
CO2
Labile Root C
ROOT C N
Labile Root N
N
Cellulose C
Cellulose N
CO2
N
CO2
Extrac-tive C
Extrac-tive N
N
CO2
CO2
N
N
Humus C
Humus N
Lignin C
Lignin N
CO2
N

FIGURE 23


▨ CARBON
■ NITROGEN
PLANTS
1,000
800
600
400
gC/m2
30
25
20
15
10
5
gN/m2
21,600
21,800
22,000
22,200
1,230
1,235
1,240
1,245
1,250
1,255
SOIL ORGANIC MATTER
CONTROL
2 X CO2
+5 TEMP
2 X CO2 +5 TEMP
+ 0.1 N INPUT
PLANTS
11,000
10,000
9,000
gC/m2
100
80
60
40
gN/m2
6,000
7,000
8,000
9,000
580
600
620
SOIL ORGANIC MATTER
CONTROL
2 X CO2
+5 TEMP
2 X CO2 +5 TEMP
+ 0.1 N INPUT

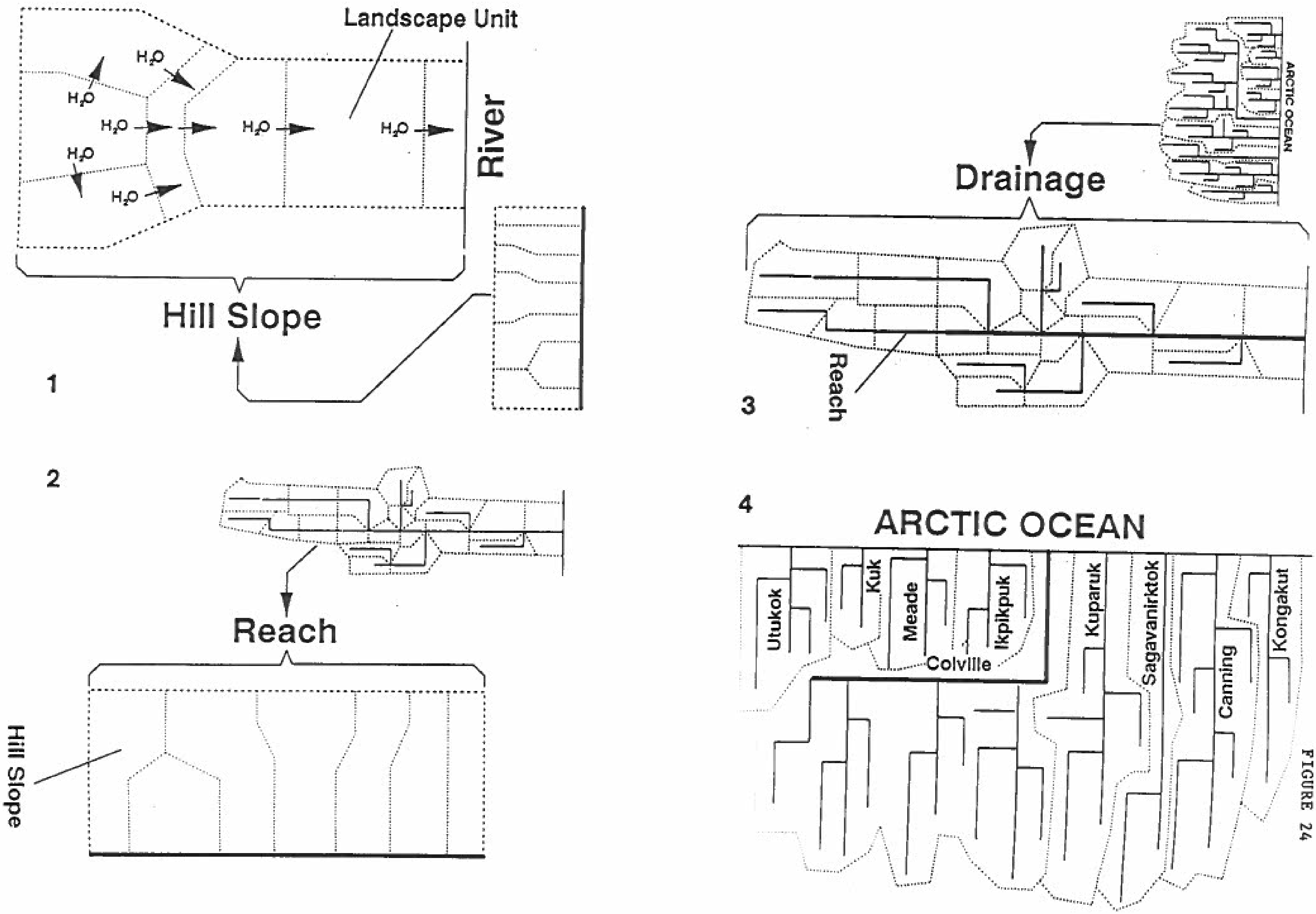
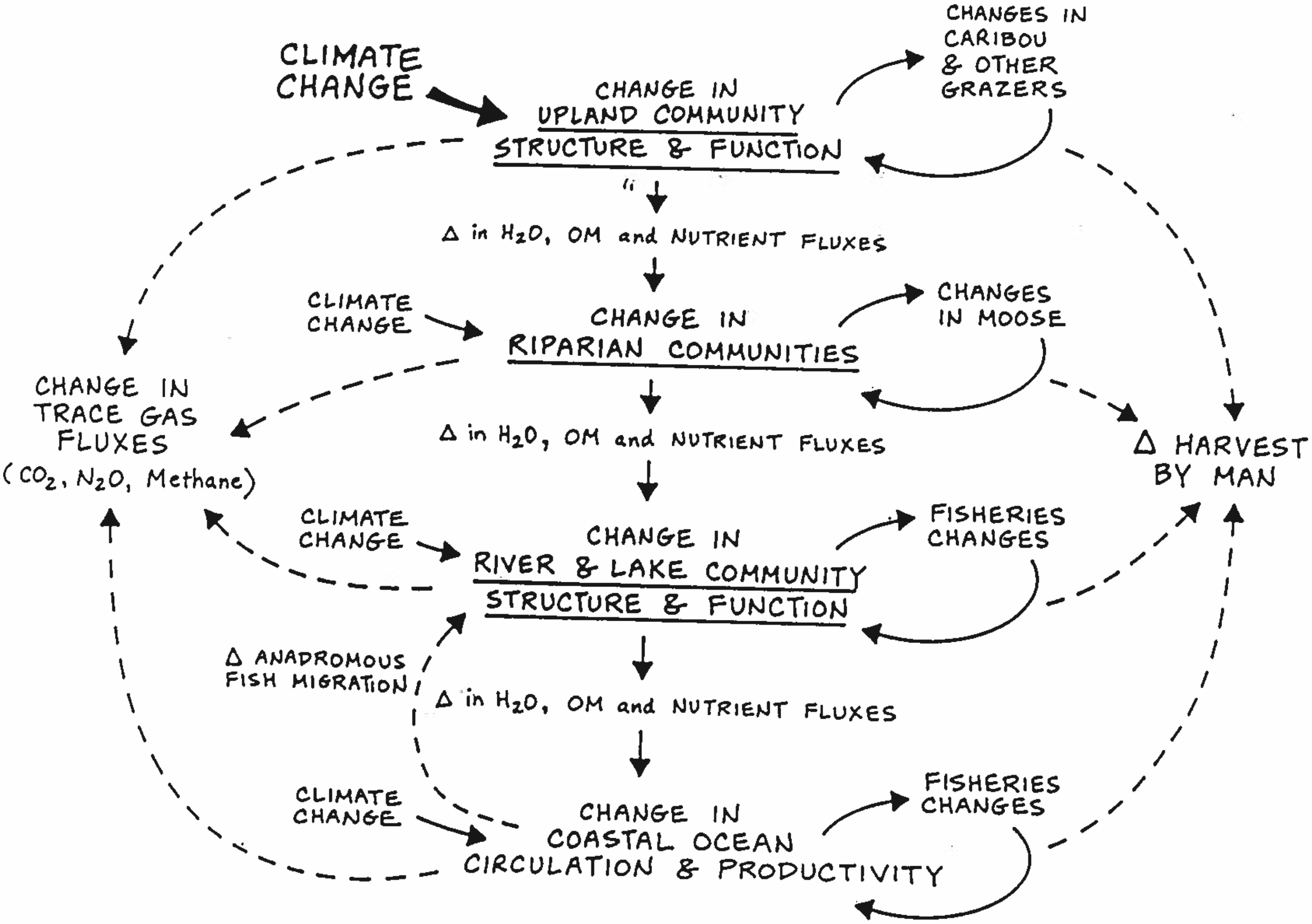

Landscape Unit
H₂O
River
Hill Slope
1
2
Reach
Hill Slope
Drainage
ARCTIC OCEAN
Reach
3
4
ARCTIC OCEAN
Utukok
Kuk
Meade
Colville
Ikpikpuk
Kuparuk
Sagavanirktok
Canning
Kongakut

FIGURE 24

FIGURE 25

INTERACTIONS OF ARCTIC COMMUNITIES AND THEIR BIOGEOCHEMICAL CYCLES WITH GLOBAL CLIMATE CHANGE



APPENDIX I : THE ARCTIC LTER DATABASE

The Arctic LTER database is a comprehensive database that contains all of the long term monitoring and experimental data from the Toolik Lake Research Site. As of April 1991, the database had 160 files compiled from 16 principal investigators. Each data file is accompanied by a documentation file to explain the contents. The documentation files and the naming of the files are standardized for ease of viewing and searching. An example and the instructions for completing the documentation form are given in the following pages. Subject searches can be conducted through this documentation. All of the data and the documentation files that are approved for general distribution are accessable to the public (Figure 1). A user-friendly program is available for the individual who wants to do simple queries, calculations, or graphs on the approved datasets directly on the LTER computer. Enclosed is an example of a completed documentation form (Example 1), the corresponding data set (Example 2), and a representative graph from that file (Example 3).

PROTOCOL FOR ENTERING DATA FILES INTO THE LTER DATABASE

This is a concise explanation of how the data is entered and validated as part of the LTER database. This process is continually being revised and updated to respond to the growing needs and demands on the database. The final format of the data is in Paradox 3.5 and the documentation is in ASCII. The documentation files are also stored in hardcopy.

(1) Each data and documentation file are received at the main office (Marine Biological Laboratory in Woods Hole, MA) via floppy disk or E-mail. The original files are first copied to the hard drive of the main computer. The documentation and the data are then compared to make sure they correspond. Minor changes are made only to the copy on the hard drive (leaving the original unaltered). The changes to the data file are made using a spreadsheet program (Quattro Pro) and changes to the documentation file using a word processing program (XyWrite).

(2) If there are any major changes or discrepancies between the data and the documentation, the data manager will either call, E-mail, or write to the principal investigator (PI) and ask for a data reevaluation. The process will begin again on the newer version of the file. (Go back to 1)

(3) After all corrections are made, the data file is translated into Paradox 3.5 (a relational database program) and locked so that no further editing can be performed on the file. This prevents accidentally changing or deleting anything in the file.

(4) After the final versions of the data files are archived in the computer, they are separated according to their availability status.

Availability Status is defined as follows:

Type 1: Published data and 'meta-data' (data about data) are available upon request

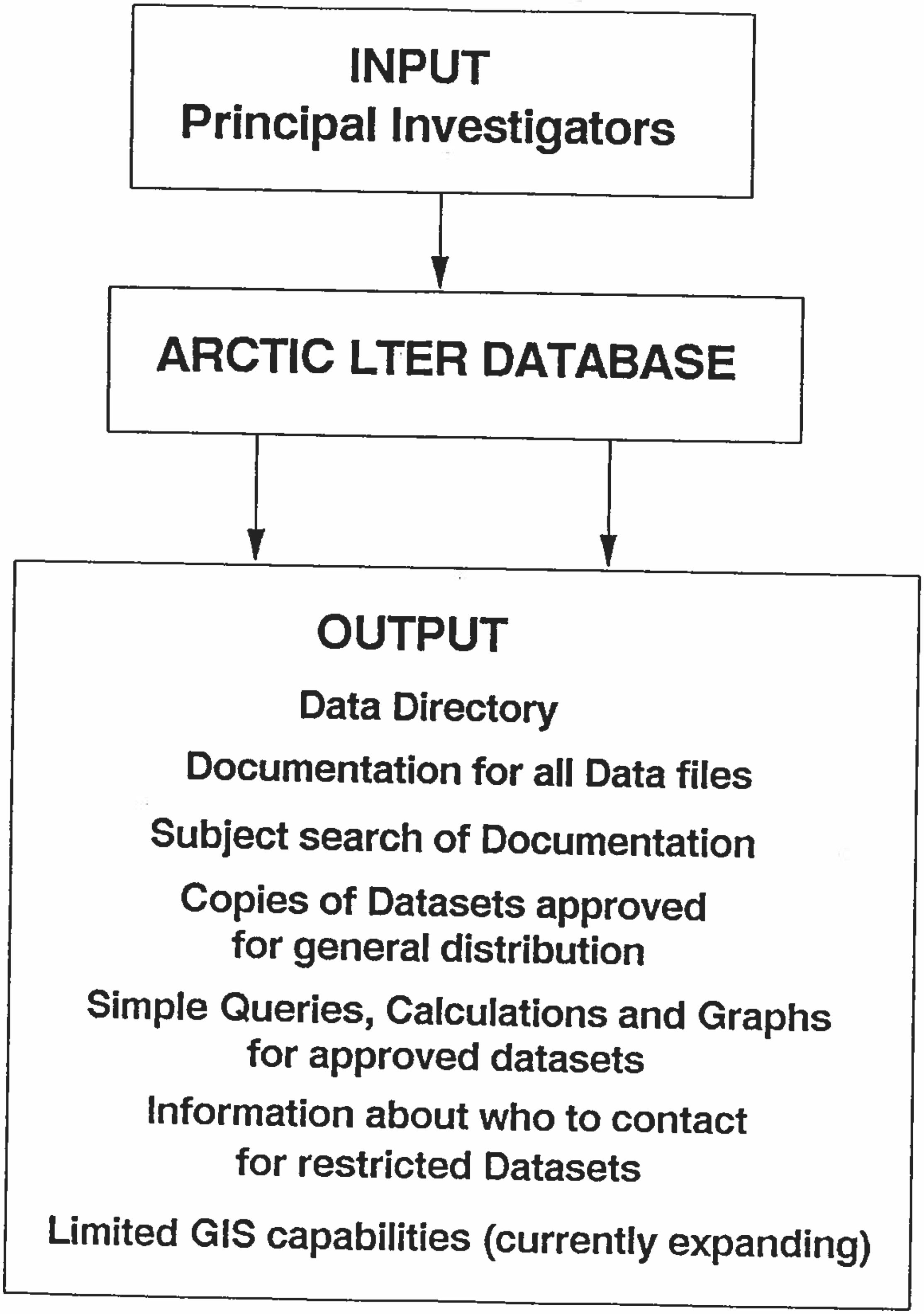
Type 2: Collective data of LTER site (usually routine measurements). Available 1 year after data are generated.
Type 3: Data from individual investigators (experimental data). Available 1 year after the termination of the grant or with permission of the investigator.
Type 4: Unusual long-term data collected by individual investigators. Available with permission of the investigator.

DATA STORAGE INFORMATION

The data is stored on a 200 Megabyte hard drive in an IBM compatible computer that is located at the Toolik Lake Arctic LTER field station during the summer and in Woods Hole during the winter. The data and documentation files are backed up on both floppy disks and the Sun Spark Unix system in Woods Hole. The Sun Spark machine can be accessed by using telnet. As of April 1991, there are 160 data files entered into the database.

NOTE: The data manager does not validate the accuracy or precision of the data (but they do try to note any large discrepancies). The PI's are responsible for making sure that the data submitted into the database is accurate.

Figure 1


INPUT
Principal Investigators
ARCTIC LTER DATABASE
OUTPUT
Data Directory
Documentation for all Data files
Subject search of Documentation
Copies of Datasets approved for general distribution
Simple Queries, Calculations and Graphs for approved datasets
Information about who to contact for restricted Datasets
Limited GIS capabilities (currently expanding)

Example 1

ARCTIC LTER DATABASE

(1) FILE NAME: 86PEKTMP.WQ1

(2) YEAR: 1986

(3) PI: B.J.Peterson

(4) OTHERS: Bernie Moller, John Helfrich

(5) BRIEF DESCRIPTION OF DATA FILE: Temperature data for the Kuparuk River for June-August 1986.

(6) KEYWORDS: Kuparuk, river, temperature

(7) SITE TYPE: AQUATIC-STREAMS

(8) RESEARCH LOCATION: The Kuparuk River crossing at the Dalton Highway.
68 38'15"N, 149 25'30"W

(9) EXPERIMENTAL METHODS: Temperature readings were taken daily with a 12" blunt stem reotemp dial-head thermometer at a location between the two culverts on the upstream side of the road.

(10) NOTES AND COMMENTS: There are several days for which no temperature data are available. There are also days on which more than one temperature reading was taken.

(11) VARIABLE DESCRIPTION:

Variable	Variable descrip.	Precis./Units	Coded (Y/N)	Missing Values
SITE	site of measurement		y	
D/D	distance from 1984 dripper	0.01 km	n	
DATE	Date	DDMMMYY	n	
DAY	Julian day	1 day	n	
HOUR	Hour of reading	2400	n	
TEMP	temperature	0.1 degrees C	n	-9999
Tmax	Maximum Temperature	0.1 degrees C	n	
Tmin	Minimum Temperature	0.1 degrees C	n	

(12) CALCULATIONS

Variable	Formula
none	

(13) FOR MORE INFORMATION, CONTACT: B.J.Peterson
MBL - Ecosystems Center
Woods Hole, Mass. 02543

(14) OTHER DATA FILES TO REFERENCE:
85PEKDIS

(15) REFERENCE CITATIONS:

(16) FORMAT OF VARIABLES:
File Name: 85PEKTMP.WQ1
File Type*: quattropro

Column No.	Column Name	Type	Width	Decimals
1	SITE	NUMERIC	1	0
2	D/D	NUMERIC	3	1
3	DATE	DATE	9	
4	DAY	NUMERIC	3	0
5	HOUR	NUMERIC	4	0
6	TEMP	NUMERIC	6	1
7	TMAX	NUMERIC	6	1
8	TMIN	NUMERIC	6	1

* The order of preference for type of data files that are submitted.
1) Dbase (.DBF)
2) spreadsheet - i.e. Lotus (.WK1)
3) Ascii (.PRN) Please specify format.

(17) NUMBER OF RECORDS: 40 records

(18) STATUS: Type 1

---

(19) FOR ARCHIVAL USE:
DATE RECEIVED: Feb90
DATA FILE ENTERED BY: Carolyn Bauman and Julie Pallant
DATA FILE VALIDATION:
NAME:
DATE:

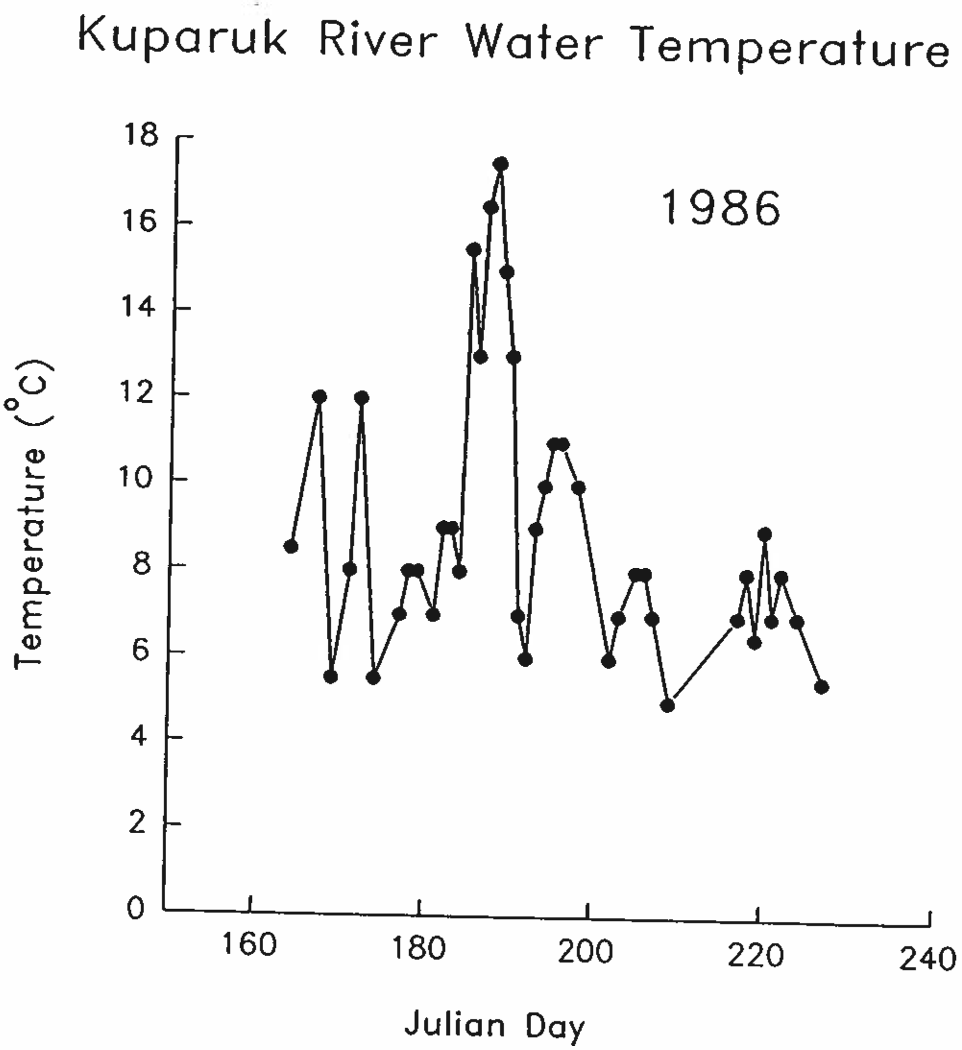
LOG OF CHANGES AND COMMENTS:

Example 2

File: 86PEKTEMP

Site	D_d	Date	Day	Hour	Temp_c	Tmax	Tmin
1	1.2	6/13/86	164	1200	8	-9999	-9999
1	1.2	6/13/86	164	2300	9	-9999	-9999
1	1.2	6/16/86	167	1500	12	-9999	-9999
1	1.2	6/18/86	169	1735	5.5	12	4.5
1	1.2	6/20/86	171	1000	8	13	5
1	1.2	6/21/86	172	2100	12	12	6
1	1.2	6/23/86	174	1700	7	13	6
1	1.2	6/23/86	174	2000	4	7.5	4
1	1.2	6/25/86	176	1400	-9999	6	3.5
1	1.2	6/26/86	177	1000	7	8.5	5
1	1.2	6/27/86	178	1600	8	10	6
1	1.2	6/28/86	179	900	8	10	6
1	1.2	6/30/86	181	1000	7	13	5
1	1.2	7/01/86	182	900	9	11	7
1	1.2	7/02/86	183	1615	9	14	9
1	1.2	7/03/86	184	1100	8	12	7
1	1.2	7/04/86	185	1100	15.5	15.5	7.5
1	1.2	7/05/86	186	1100	13	15.5	7.5
1	1.2	7/06/86	187	1100	16.5	18.5	12
1	1.2	7/07/86	188	1100	17.5	21	10
1	1.2	7/08/86	189	1100	15	18	12
1	1.2	7/09/86	190	1100	13	19	11
1	1.2	7/10/86	191	1100	7	8	7
1	1.2	7/11/86	192	1100	6	7	5
1	1.2	7/12/86	193	1100	9	10	6
1	1.2	7/13/86	194	2200	10	11	8
1	1.2	7/14/86	195	1600	11	12	8.5
1	1.2	7/15/86	196	1300	11	11	8
1	1.2	7/17/86	198	1300	10	11.5	7
1	1.2	7/19/86	200	1630	-9999	9.5	6
1	1.2	7/21/86	202	900	6	8	5
1	1.2	7/22/86	203	1230	7	7	4
1	1.2	7/24/86	205	1230	8	11	5.5
1	1.2	7/25/86	206	1230	8	9	7
1	1.2	7/26/86	207	1230	7	9	6
1	1.2	7/28/86	209	300	5	7	4
1	1.2	8/05/86	217	1900	7	11	-9999
1	1.2	8/06/86	218	900	8	8.5	6.5
1	1.2	8/07/86	219	930	6.5	8.5	5.5
1	1.2	8/08/86	220	1130	9	9	7
1	1.2	8/09/86	221	900	7	9	7
1	1.2	8/10/86	222	1400	8	9.5	6.5
1	1.2	8/12/86	224	1800	7	11	7
1	1.2	8/15/86	227	1200	5.5	10	5

Example 3


Kuparuk River Water Temperature
1986
Temperature (°C)
0
2
4
6
8
10
12
14
16
18
160
180
200
220
240
Julian Day

ARCTIC LTER DATABASE

28-Mar-91

INSTRUCTIONS FOR COMPLETION OF DOCUMENTATION FILE

In each section of the .DOC file additional spacing may be added or deleted as needed.

(1) FILE NAME: This name will be assigned by the PI. (Please be consistent within the File Naming System for the LTER database).

(2) YEAR: The year that the data was collected.

(3) PI: Fill in the name of the PI responsible for the data collection.

(4) OTHERS: PIs, RAs or Techs who were also involved in the data collection or compilation.

(5) BRIEF DESCRIPTION OF DATA FILE: Short, accurate explanation of what the data set is.

(6) KEYWORDS: Words that may be helpful in cross-referencing or cataloging the data. These should be in lower case format, unless the word is a proper name.

(7) SITE TYPE: This should be one of three types: TERRESTRIAL, AQUATIC-LAKES or AQUATIC-STREAMS.

(8) RESEARCH LOCATION: The name of the sampling location. Remember to include not only the name, but, when necessary , details and descriptions of the sampling location. Examples would be specific reaches of rivers, sections of lakes, treatment areas (treatment or control side of Lake N-2, mouth of the Kuparuk River, near Green Cabin Lake in the headwaters of the Kuparuk River, limnocorrals), map coordinates, nearby landmarks, or any other details that may help someone reference that particular location.

(9) EXPERIMENTAL DESIGNS AND METHODS: The description of methods should be fairly detailed and include any literature references (including author, title, journal and page numbers) pertaining to the methods.

(10) NOTES AND COMMENTS: Notes and comments about the data can go in two different places. Those with reference to the whole data set, including explanations of any problems with data collection or the data set, or reasons for missing data should be placed in this section. Comments about individual data points will not normally be included here, but will be placed in the actual data file (see first paragraph under VARIABLE DESCRIPTION below).

(11) VARIABLE DESCRIPTION: This section describes the variables in the data set. Variable names must be less than 8 characters. The Variable Description should be a brief explanation of what the variable name represents.

The variables Site, Date and Comments must be included in every data file. The variable Site is a numerical 3 digit code and should be taken from the Site Name Code List (enclosed). If you have a new site that is not on the list, do not code it yourself; ask the data manager to add it to the master list. Comments must be the last column in the file, and is the column in which comments about individual data points are placed. All Comments for a data point must be entered on a single line which can be no longer than 250 characters. The variable D/D (for depth/distance) must be included in every aquatic file, as it corresponds to the depth in a lake or the distance along a river from which a sample was taken. For those working on the Kuparuk River, D/D needs to be relative to the 1984 phosphorous dripper, and Oksrukuyik Creek should be relative to the 0.0 K dripper site set in 1989.

Variables for time in Hours are to be in 24 hour format (not am or pm) and based on Alaska Standard Time, not Alaska Daylight Savings Time. Entries should be 4 places, hours and minutes, without any punctuation (examples 0458 or 2133). Individual PIs need to responsible for making these time corrections. Precision/Units should describe the units for the data and how precise the data are. Date should be in the format DD-MMM-YY (i.e. 01-Jun-88). Coded (Y/N) is answered by a Y indicating that the variable has been coded, N indicates that it has not. The only required variable that is coded is SITE. If you code any of your own variables be sure to explain them. Any Missing Values shall be designated by BLANK in a spreadsheet/database format or a . (period) in ascii files.

(12) CALCULATIONS: Any variables that have been calculated, along with their corresponding formula(s).

(13) FOR MORE INFORMATION, CONTACT: List here the name and address of the PI, or person, most knowledgeable about the data set.

(14) OTHER DATA FILES TO REFERENCE: This is a list of other files, or work by other PIs, that you feel may be of interest to a person looking at this file.

(15) REFERENCE CITATIONS: List in proper form both the published literature, and unpublished references, relating to this data set.

(16) FORMAT OF VARIABLES: This section explains how the data file is set up.
FILE NAME: This is the name of the data file. It must be the same name as this documentation file but with the .DBF, .WK1 or .PRN extension.
FILE TYPE: The data file must be in one of the following formats, in order of preference: 1) Dbase (.DBF), 2) spreadsheet (i.e. Lotus .WK1) or 3) Ascii (.PRN). Ascii files must be comma delimited or in fixed format. Remember to specify the format.
COLUMN NO.: The column or variable must be assigned a sequential number, starting with 1 and must be in order of the variables from left to right.
COLUMN NAME: This is the variable name. It must be 8 or less characters long. It also must be listed in order of occurrence from left to right.
TYPE: Note if the variable is text, numeric, alphanumeric or date.
WIDTH: List the width of the column for the particular variable.
DECIMALS: Designate how many decimal places there are in the numeric entries.

(17) NUMBER OF RECORDS: This states how many records are in the date file that is being referenced. This ensures that no data is lost during the transition of data.

(18) STATUS: Type of Availability Status

Type 1: Published data and 'meta-data' (data about data) are available upon request
Type 2: Collective data of LTER site (usually routine measurements). Available 1 year after data are generated.
Type 3: Data from individual investigators (experimental data). Available 1 year after the termination of the grant or with permission of the investigator.
Type 4: Unusual long-term data collected by individual investigators. Available with permission of the investigator.

(19) FOR ARCHIVAL USE: The data manager will fill this in, noting when the file was received and who entered it into the data base. A quality control check of the data will then be made, by using summary statistics and generating a few plots. The PI will be asked to check these and validate the accuracy of the data in the database file. The name of the data confirmation person and the date of confirmation will be recorded, and any changes made to the file will be logged.

Feb. 12, 1990

HOW TO NAME YOUR ARCTIC LTER DATABASE FILES

File names must be 8 characters long with an appropriate extension designating documentation or data, as shown below.

_ _ _ _ _ _ _ _.DOC or _ _ _ _ _ _ _ _.WK1
1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8

Spaces 1 and 2 designate the year. Some historical datasets may have data for several years, in that case, spaces 1 and 2 should be the most recent year represented in the dataset.

Spaces 3 and 4 designate the source of the dataset. In most cases these are the first two letters of the P.I.s last name (see below to find your individual designation).

Spaces 5, 6, 7 and 8 are to be filled in by the P.I. to complete the 8 digit name. While the choice of entries for these spaces are yours, all 4 spaces must be filled in (leave no blanks). Since the file is already classified as to year of collection and source of the data, you should use these characters to convey some additional useful information about the contents of the file, as in the example below. Remember, if you contribute more than one dataset each year, you need to use these 4 digits to make unique names for your datasets within a particular datayear. It is very important to make sure that the name that you create is not duplicated for another dataset.

Also remember that the documentation file and the data file for a particular dataset must have the same name with the appropriate corresponding extension.

Example: 88MITNUT.DOC

This file name indicates that:	This is the documentation file for a 1988 Miller dataset, w/ Miller's designation for Toolik Lake Nutrient data.

Feb. 9, 1990

CODES FOR FILE NAMING SYSTEM

Two letter Code	Data Source
BO	Bowden
DL	Dr. Data Logger
DE	Deegan
FR	Fry
GI	Giblin
HE	Hershey
HO	Hobbie
KI	Kipphut
KL	Kling
LA	Drs. Landscapes
LI	Linkins
MC	McDonald
MI	Miller
NA	Nadelhoffer
OB	O'Brien
PE	Peterson
RA	Rastetter
RU	Rublee
GS	Shaver
SH	Shell
WA	Walker

If you don't find your name on the list or if there is more than 1 person responsible for the data (as in the Landscape project) consult the Arctic LTER Database Management team for a two letter code.

CATALOG OF LONG-TERM DATASETS

RIVERS: **KUPARUK RIVER**

DISCHARGE	1983-1990
NUTRIENTS	1987-1990, ND 1983-86
PHYSICS AND CHEMISTRY(pH, ALKALINITY, TEMPERATURE, CONDUCTIVITY, CATIONS AND ANIONS)	1988-1990, ND 1983-87
SESTONIC AND EPILITHIC CHLOROPHYLL	ND 1983-90
FISH GROWTH, LENGTH AND WEIGHT	1985-1990
INSECTS	1989, ND 1988, 1990
ISOTOPES	1988

OKSRUKUYIK RIVER

DISCHARGE	1988-1990
NUTRIENTS	1990, ND 1989-90
PHYSICS AND CHEMISTRY(pH, ALKALINITY, TEMPERATURE, CONDUCTIVITY, CATIONS AND ANIONS)	ND 1989-90
SESTONIC AND EPILITHIC CHLOROPHYLL	ND 1989-90
FISH GROWTH, LENGTH AND WEIGHT	1989-1990
INSECTS	1989, ND 1990
ISOTOPES	

LAKES: **TOOLIK LAKE**

PHYSICS AND CHEMISTRY (OXYGEN, TEMPERATURE, CONDUCTIVITY, pH, ALKALINITY, LIGHT, SECCHI DEPTH, CATIONS AND ANIONS)	1975-1981, 1983-1990
NUTRIENTS	1975-1981, 1983-1990
SESTONIC CHLOROPHYLL	1975-1981, 1983-1990
PRIMARY PRODUCTION	1975-1981, 1983-1990
ZOOPLANKTON	1989, ND 1975-1990
INSECTS	ND 1988-1990
FISH GROWTH, LENGTH AND WEIGHT	1986-1989
TOOLIK LAKE INLET DISCHARGE	
ISOTOPES	1987-1989

LAKE N-2

PHYSICS AND CHEMISTRY (OXYGEN, TEMPERATURE, CONDUCTIVITY, pH, ALKALINITY, LIGHT,SECCHI DEPTH, CATIONS AND ANIONS)	1986-1989, ND 1990
NUTRIENTS	1986-1990
SESTONIC CHLOROPHYLL	1986-1989, ND 1990
PRIMARY PRODUCTION	1986, 1988-1989, ND 1990
ZOOPLANKTON	ND 1983-1990
INSECTS	ND 1988-1990
FISH GROWTH, LENGTH AND WEIGHT	1987-1989, ND 1985-87, 1990
ISOTOPES	1987-1989

LAKE I-8

PHYSICS AND CHEMISTRY (OXYGEN, TEMPERATURE, CONDUCTIVITY, pH, ALKALINITY, LIGHT, SECCHI DEPTH, CATIONS AND ANIONS)	1990, ND 1986, 1989

NUTRIENTS	ND 1986, 1989-90
SESTONIC CHLOROPHYLL	ND 1986, 1989-90
PRIMARY PRODUCTION	ND 1986, 1989-90
ZOOPLANKTON	ND 1986, 1989-90
INSECTS	ND 1986, 1989-90
FISH GROWTH, LENGTH AND WEIGHT	1989, ND 1986, 1990

TERRESTRIAL: MESIC TUSSOCK TUNDRA, HEATH, WET SEDGE, SALIX SHRUB SITES

FLOWERING DATA ALONG THE HAUL ROAD TRANSECT	1977-1990
NITROGEN MINERALIZATION	1988-1990, ND 1986-1990
WEIGHT PER TILLER (*Eriophorum vaginatum*)	1977-1990
PLANT BIOMASS	ND 1985, 1988, 1989
RAIN CHEMISTRY (pH, NUTRIENTS)	1990, ND 1988-89

WEATHER STATIONS:

TOOLIK LAKE, TOOLIK MESIC TUSSOCK TUNDRA, KUPARUK CROSSING, KUPARUK HEADWATERS, SAGAVANIRKTOK RIVER HEATH

AIR TEMPERATURE (MAX, MIN AND AVERAGE)	1988-1990
WIND (SPEED, DIRECTION)	1988-1990
RELATIVE HUMIDITY	1988-1990
PRECIPITATION	1988-1990
PHOTOSYNTHETIC ACTIVE RADIATION (PAR)	1988-1990
NET RADIATION	1988-1990
SOLAR RADIATION	1988-1990
SOIL TEMPERATURE (DIFFERENT DEPTHS)	1988-1990
BAROMETRIC PRESSURE	1990
TOOLIK LAKE TEMPERATURE	1988-1990
TOOLIK LAKE DEPTH	1988-1990
KUPARUK RIVER LEVEL	1988-1990

ND= Not yet available in LTER Database as of April 1, 1991

APPENDIX II: SITE DESCRIPTIONS and RESULTS OF LAKE AND STREAM RESEARCH

Toolik Lake

Toolik Lake (68° 38'N, 149° 36'W) is a kettle lake set in a terminal moraine of the late Wisconsin Itkillik II glaciation. It is located in the foothills of the Brooks Mountains at 720 m elevation, some 20 km north of the mountains and near the Haul Road or Dalton Highway. Colinvaux reports that the oldest sediments have a radiocarbon age of 12,400 years old. The morainal material around the lake is composed mostly of Devonian conglomerates of the Chandler formation and Cretaceous sandstones. These moraines extend into the lake itself where they form reefs which divide the lake into several rather discrete basins (Miller et al. 1986). Tussock and upland heath tundra, and an occasional balsam poplar, dominate the vegetation-covered hills of the watershed.

The Toolik watershed covers 65 km^2 and the lake 1.49 km^2 (lake vol. 10.6 x 10^6 m^3, max. depth 25 m, mean depth 7 m). The major inlet drains 75% of the watershed including a series of 12 lakes. A secondary inlet drains another 7% of the watershed and several ephemeral streams account for the remainder of the inflow. The volume of the inflow is enough to flush the lake about once each year (Hobbie et al. 1983); much of the flow comes from snowmelt in mid- to late-May to early July. Ice-out in the lake occurs from mid to late June. The lake level fluctuates by as much as 59 cm, is generally highest at the time of major inflow, and declines throughout the summer.

The average monthly summer air temperature varies from 5 to 14°C while the summer rainfall varies from 30 to 40 mm. The average annual temperature is -10°C and the annual precipitation is 200-400 mm. Most of the precipitation occurs as snowfall.

The surface water temperature reaches 18°C but the volume-weighted summer temperature is 10-14°C (Miller et al. 1986); the lake is dimictic despite its northern location. Ice cover, which may reach 1.4 m thick, forms in early October. The lake first stratifies in July when the thermocline is located at 5 m. By early August, thermocline depth is at 7 m and the lake mixes in late August. The lake is fairly clear with summer Secchi disk readings around 6-7 m.

The chemistry of Toolik Lake is typical of oligotrophic lakes. Oxygen is generally near saturation even during summer stratification and during the long arctic winter. The alkalinity is 0.2-0.4 meq l^{-1} and summer pH is around 7.6 but winter pH's may be lower (Whalen and Cornwell 1985). Plant nutrients are extremely dilute because of the low annual loadings of 290 mmol N m^{-2} total dissolved nitrogen and 4.64 mmol P m^{-2} total phosphorus. Average lake concentrations of nitrogen and phosphorus are 0.4 μM NO_3-N, 0.2 μM NH_4-N, and 0.2 μM total phosphorus (Whalen and Cornwell 1985).

The low levels of plant nutrients lead to low levels of phytoplankton biomass and productivity. Photic zone chlorophyll averages around 2 ug l^{-1} and phytoplankton primary productivity averages about 1 mol C m^{-2} yr^{-1} (Miller et al. 1986). The phytoplankton in Toolik Lake are sparse and small, around 2 x 10^6 cells l^{-1} and generally less than 6 μm in diameter. Most of the algae are flagellates belonging to the Chrysophyceae and Cryptophyceae. There are some planktonic centric diatoms (*Cyclotella compta* and *C. bodanica*) which are also quite small (Miller et al. 1986). Bacteria numbers, commonly 1.5 x 10^6 ml^{-1} (Hobbie et al. 1983), are close to the average for natural waters.

The zooplankton densities in Toolik Lake are also quite low (O'Brien et al. 1979). The most common species are Bosmina longirostris, Daphnia longiremis, Diaptomus pribilofensis and Cyclops scutifer. The Bosmina occasionally reach 10 per liter but are commonly 1-5 per liter as are the other three species. An invertebrate planktivore, Heterocope septentrionalis, is a very important predator on these herbivorous species but is rarely more abundant than 0.3 per liter. Surprisingly, rotifers are very rare and are of no quantitative significance in Toolik Lake.

The benthic environment consists of soft sediments (75%) and rocks (25%, around the shoreline and on the reefs). In shallower areas, the soft sediments may be covered with patchy beds of diminutive macrophytes (mosses and Nitella). The benthic invertebrate fauna is dominated by chironomids including at least 27 species spread among 21 genera, and by molluscs (Hershey 1985b). These include two clams (Pisidium and Sphaerium) and four snails (Lymnaea elodes, Valvata lewisi, Gyraulus sp., and Physa sp.). Larval caddisflies and oligochaetes also occur but are quite sparse.

Five species of fishes are present in Toolik Lake. Juvenile lake trout (Salvelinus namaycush) and round whitefish (Prosopium cylindraceum) may feed on zooplankton, but adults feed on benthos or other fish in the case of lake trout (O'Brien et al. 1979). Arctic grayling (Thymallus arcticus) are relatively common and feed on zooplankton when small but become fairly omnivorous when longer than 15 cm. The slimy sculpin (Cottus cognatus) is quite common in the rocky littoral and soft-sediment zones (McDonald et al. 1982) and feeds entirely on benthic invertebrates (Cuker 1981, Hershey 1985, Hershey and McDonald 1985). The adult burbot (Lota lota) have been observed to feed on fish, including sculpin.

Kuparuk River

The Kuparuk River, a clear-water tundra river, rises in the foothills of the Brooks Range and flows north-northeast. Our study site is from its headwaters to 5 km below its intersection with the Haul Road. The river down to this point has a main channel length of 25 km, drains an area of 143 km^2, and has an average channel slope of 3.13%.

The upper basin of the Kuparuk River has a similar glacial history to that of Toolik Lake. The upper layers of the soils consist of 30 to 70 cm of peat underlain by alluvial and glacial deposits of coarse sand and gravel. Permafrost is present throughout the area to a depth of up to 800 m; the mean thawed depth of the active layer is about 40 cm during August (K. R. Everett, pers. comm.).

The vegetation of the upper basin consists of alpine communities at the higher elevations and moist tundra communities, predominantly the cotton grass Eriophorum vaginatum, in the foothills. Along the stream banks there are patches of dwarf willows and birches, some reaching 1 m in height.

The average annual total precipitation in the foothills of the Brooks Range is around 15 to 25 cm. Approximately half of the precipitation falls as snow on the upper basin from September through May and the melting of this snow causes the spring flooding. Summer water temperatures may reach 20°C and average 8-10°C. Stream discharge has ranged from 0.3 to 28.3 $m^3\ sec^{-1}$ and the total suspended sediment load ranged from 0.4 to 35 $mg\ l^{-1}$. Flow nearly ceases by late September and the riffles become dry. The pools freeze solid in October and there is no flow until mid to late May.

Nutrients are low in the surface waters of this pristine watershed. Typical mean annual values are 0.8 μM NH_4-N, 1.5 μM NO_3-N, 18 μM DON-N, 0.3 μM total dissolved PO_4-P, and 0.2 μM fine particulate P. Nitrate concentrations are inversely correlated with flow whereas particulate phosphorus concentrations increase during high flows. Export from the watershed during 1980 was estimated to be 335, 232, and 6,500 mol km^{-2} yr^{-1} NO_3-N, NH_4-N and DON-N, respectively, and 92 and 98 mol km^{-2} yr^{-1} of TDP-P and fine particulate P.

About 92% of the total organic carbon export is dissolved organic carbon (Peterson et al. 1986). The remaining 8% is particulate carbon (fine is 7% and large is 0.7%). The lateral input of carbon from the tundra is mostly in the form of peat because there is little movement of litter from the tundra surface; estimated input from bank erosion ranged from 17 to 25 mol C m^{-2} yr^{-1}. The detritus (particulate organic carbon) on the river bottom equals 2.3 mol C m^{-2} while epilithic algal biomass is 0.02 mol C m^{-2} and net primary production averages about 1 mol C m^{-2} yr^{-1}.

The insect community in the river is dominated by four species. Black flies, predominantly Prosimulium martini, account for the major portion of secondary production in the river. Baetis lapponicus, the most abundant mayfly, contributes about 10 to 20% as much production as the black flies. The dominant chironomid is Orthocladius rivulorum. The next most important insect is Brachycentrus americanus, a caddisfly that contributes about 1% of the secondary production in the river.

The fish community has only one species, the arctic grayling (Thymallus arcticus), which feeds mainly on drifting insects and particulate matter although they also forage on pool bottoms. We commonly observe from two to five adult grayling (30-40 cm) in each pool. During the late summer, grayling move upstream to a headwater lake where they overwinter. Young-of-the-year (YOY) grayling exhibit high annual variations in abundance. In a good year, such as 1990, there may be as many as several hundred per pool. They are drift feeders almost from hatching, but also take food off the bottom.

The Kuparuk River is similar to many temperate streams in that allochthonous carbon inputs dominate the carbon cycle in the river in spite of the absence of shading vegetation. Much of this carbon is more refractory than the leaf and litter input to temperate streams. The standing stocks of chlorophyll on the rocks and the levels of gross and net primary productivity are low in comparison with temperate streams; apparently this occurs because of phosphorus limitation and the short growing season. The export of organic carbon from the watershed is about average for rivers but because the Kuparuk watershed has low terrestrial net primary productivity, the percentage of the total watershed organic carbon production exported via the river is relatively high (2-6%). Dissolved organic carbon is over 90% of the total export. The Kuparuk thus has a combination of characteristics which make it similar in some respects, but quite different in others, to boreal and temperate streams.

LAKE RESEARCH RESULTS.

Description of Research and of Response Scheme. Here, we present results and predictions of responses of the Toolik Lake flora and fauna to changes in nutrients and predators. The information comes from three sources: measurements in Toolik Lake; limnocorral experiments (60-70 m^3 volume) in a bay of Toolik Lake; and a fertilization experiment in Lake N-2, a small 11 m deep lake divided by a plastic curtain. An overview and synthesis of the responses of Toolik Lake biota to the addition of nutrients and to a decrease in the size and abundance of the top predator, lake trout, is given in Fig. 1. The bottom-up effects of nutrients as they propagate through the ecosystem are diagrammed flowing from left to right. The top-down or feedback effects are diagrammed flowing from right to left. Each step is numbered, described, and documented below.

Bottom-up (resource) controls. The results and predictions of responses to a change in resource levels are given in step numbers 1-20 (Fig. 1).

Response of nutrients and algae (#1,2). Bioassays in Toolik show that photosynthesis is first limited by low levels of light and biomass under the ice, then by P shortly after ice out in late June, then by a co-limitation of N+P in early July and August. We confirmed this in the limnocorral where added nutrients induced an immediate increase in phytoplankton growth and biomass (Fig. 2). The response also occurred in a bigger system (addition experiments in divided Lake N-2). The long-term data set from Toolik Lake indicates that primary productivity varies directly with the river flow in the Kuparuk River (Fig. 3); the trend suggests that P in the river input is the most important control.

Response of grazing and predatory zooplankton (#3,4). The limnocorral experiments showed an unexpected one year lag in response of the zooplankton to the fertilization. This also occurred in the whole lake (N-2) experiment and all the zooplankton except Cyclops doubled their abundance. We examined the lack of close coupling to the planktonic food web shown by the Cyclops by labeling the algae with ^{15}N in the fertilized lake. The zooplankton, presumably eating ^{15}N-labeled algae, became enriched in ^{15}N over the summer. Cyclops contained less label than Daphnia or Diaptomus at the end of the experiment, consistent with their apparent weak link to algal production.

Feeding experiments in various sized containers have shown Heterocope to be a voracious predator on small-bodied zooplankton. Analyses of the natural abundance of stable N isotopes (delta ^{15}N) show that this species is mixotrophic (can also be grazers). In Toolik the delta ^{15}N shift between Heterocope and small-bodied zooplankton is 2 o/oo (Fig. 4) indicating they are predators most of the time and that their major food source is probably zooplankton. But in several ponds and lakes near Toolik Lake, Heterocope had a shift of only 1 o/oo from the small-bodied zooplankton, indicating that algae are a major food source in these systems. Heterocope is present in Lake N-1 where an experimental fertilization is now underway (begun 1990), so we will collect more information on the response of the predatory zooplankton to fertilization.

Fish growth response (#5,6,14). The fish in ultra-oligotrophic Toolik Lake grow slowly; lake trout 35 years old weigh only 1.5 kg. As in other northern lakes, the lake trout subsist first on zooplankton, then, as they grow, they subsist on benthic invertebrates. Finally, a small part of the population makes a trophic jump to piscivory. At Toolik, the invertebrate food is snails whereas in other more northern lakes it is caddisfly larvae and amphipods. The field data indicate that piscivory begins at 35 cm in length; an energetic model confirms that if they continue to eat snails, their body size can never exceed 800 g even though they may live more than 50 years (Fig. 5). The effect is really size dependent in that the closer an individual fish approaches to 800 g, the poorer its condition should be. We have tentative field corroboration of the model for lake trout in Toolik Lake because condition factors for these fish have increased from 1977 to 1986 while their size declined from 578 g in 1977 to 318 g in 1986 (Table 1; McDonald and Hershey 1989). The decline in size was caused by sport fishing.

The ^{15}N content of these fish confirm that lake trout first eat a planktonic food, perhaps at the third trophic level, then eat at the second trophic level (snails); a few large fish eat at the fourth trophic level (Fig. 6). Based on these data, it is likely that lake trout will grow faster in a more productive ecosystem. We plan to test lake trout response to a better food by introducing cisco (whitefish) into a lake with lake trout. Cisco specialize on zooplankton and will be a better forage fish for lake trout than grayling.

Sediments trap nutrients (#7,8) but benthic algae increase. The iron-rich sediments (5-10% Fe) in the lakes of the Toolik region are quite unusual in their nutrient sorbing properties as phosphorus is apparently very tightly bound and cannot be recycled to the overlying waters under either aerobic or anaerobic conditions. In the fertilized side of Lake N-2 just after ice out (Fig. 7), for example, the bottom water was anoxic but even though this system had been fertilized with phosphate for the previous three summers no phosphate had returned from the sediments overwinter. This iron-bound PO_4 is available through equilibrium reactions only to benthic algae (the equilibrium reaction will produce a small amount of phosphate in the interstitial water) and we have measured a 2-3 fold increase of benthic algal productivity in the fertilized side of Lake N-2. Therefore, we predict an increase in benthic algae when more nutrients are added to the water. This phenomenon of nutrient binding in sediments should allow a rapid recovery from eutrophication caused by external nutrients. We will test this by ceasing to fertilize Lake N-2 and measuring the rate of recovery to the pre-fertilization conditions. The proposed research in Lake N-1 will replicate the N-2 experiment on the role of sediments and the response of benthic algae to fertilization.

Chironomids and sculpin do not respond to eutrophication (#9,10,11). At the level of fertilization we have applied in Lake N-2, the chironomids did not respond even after benthic algal productivity had doubled and redoubled. We conclude that sculpin predation is intense enough to maintain chironomid density below the level at which they would be food or resource limited. Also, lake trout will not obtain extra food from sculpin during eutrophication of these lakes. This interesting finding requires more work and confirmation in another lake. We will add sculpin to Lake E-1 (no sculpin, abundant chironomids) and remove sculpin from Lake N-3 (sculpin, few chironomids) to test the intensity of the linkage and of the controls.

Snails will increase during eutrophication with a consequent increase in lake trout growth (#13,14). For snails, abundance appears to be limited by an interaction of lake trout predation and resource competition. When lake trout are absent, snails are very abundant and fertilization stimulates growth of the snail Lymnaea. But whether Lymnaea density will be stimulated in a fertilized lake containing lake trout remains to be determined (experiment continuing in Lake N-1).

DOC and DON from outside Toolik Lake is probably used by microbes and drives a microbial food web (15,16,17,18,19). A nutrient budget for Toolik Lake (Table 2, 3) illustrates the importance of the DON input to the total nitrogen budget and the importance of DON to the net input to the lake. If the DON retained in the lake is really transformed into inorganic N and made available to algae, it would supply 75% of the nitrogen needed for photosynthesis. This DON budget needs to be redone with the modern methods of Sugimura and Suzuki (1988). With the same reasoning, the amount of organic carbon retained in the lake is about the same quantity as the measured planktonic primary productivity. The DOC budget also needs to be redetermined using the new Sugimura and Suzuki method.

The only information on usability of the DOC+DON comes from our stream research where microbes did attach and grow when glass slides were incubated in the dark in the flowing Kuparuk River. An educated guess, based upon the relatively high numbers of bacteria in Toolik, is that the DOC+DON does contribute to bacterial growth. The relationship needs to be quantified in Toolik, and indeed has never been quantified in any lake.

Our evidence for the strong linkage between algal and bacterial production comes from the limnocorral experiment (Hobbie and Helfrich 1988) in which the bacteria numbers and production were measured each day in a fertilized corral. The chlorophyll a increased 10-20 fold, the bacterial numbers increased 4-fold, and the bacterial production increased about 8-fold. The production rates of 10^6 cells ml^{-1} d^{-1} are high for arctic lakes and are similar to temperate system rates. It is also evident in the figure that flagellate numbers and production increased in response to the increased bacterial production.

Certainly if there are higher numbers of flagellates, then more carbon will be transferred to zooplankton grazers. In an experiment in a limnocorral (10 m^3) in Lake N-2, leucine-^{13}C was added weekly to the water. By the end of the summer, the large zooplankton were quite heavily labeled with ^{13}C. This indicates that either the zooplankton consume bacteria directly or that there is a transfer of carbon from bacteria to flagellates to zooplankton.

<u>Top-down effects on pelagic food webs (#23,24,25,26)</u>. Since our research began in Toolik Lake in 1975, the median size of the lake trout has become smaller as a result of recreational fishing (Table 1; McDonald and Hershey 1989). From the theory illustrated in Fig. 8, we have predicted that the decrease in the size of the lake trout would result in a relaxation of the strength of the effect of lake trout on grayling, that increased grayling would decrease predatory zooplankton numbers, and that fewer predatory zooplankton would, in turn, allow small sized zooplankton to increase in numbers.

We have only qualitative information about the relaxation of lake trout pressure on grayling (predation or behavioral). It was predicted that if fishing pressure reduced lake trout densities and overall body size that grayling should become both more abundant and more numerous in the open water. In fact, we have observed that there are now many more grayling "rises" seen on a calm evening offshore in Toolik Lake than in the 1970's. Clearly we need to continue to monitor these populations in Toolik Lake. A second prediction was that large-bodied zooplankton would decline in Toolik Lake due to increased predation from grayling. Consistent with predictions, large bodied zooplankton species have dramatically declined, <u>Daphnia middendorffiana</u> by a factor of 50 and <u>Holopedium gibberum</u> by a factor of 200 (Fig. 9)

Grayling also have an effect on invertebrate predators. For example, in the 60 m^3 limnocorrals, one medium-sized grayling eliminated all of the <u>Heterocope</u> within two weeks, and five grayling eliminated <u>Heterocope</u> in less than one week. This control agrees with evidence from lake and pond surveys; large zooplankton were absent from waters where grayling were abundant but were common where grayling were scarce or absent (Luecke and O'Brien 1983, O'Brien et al. 1979). Finally, in Toolik Lake the density of <u>Heterocope</u> has decreased by about 50% since the 1970's.

There is evidence that <u>Heterocope</u>, in turn, controls the abundance of small-bodied zooplankton. The smaller zooplankton in Toolik seem to be facing severe predation pressure because Bosmina longirostis and Daphnia longiremis decline in abundance each year whereas in other lakes in the area, which lack Heterocope, populations of these two species increase throughout the summer.

Top-down effects on benthic food web (#28,29,30). Slimy sculpins, a prey of lake trout, have increased in size in Toolik Lake and are also relatively more abundant on the soft sediments and at the rock/soft sediment interface than in the past. We interpret this as evidence that the sculpin have moved out to the soft sediments now that there are fewer large lake trout. In general, chironomid densities are highest in lakes with lake trout, are lowest in lakes with sculpin as the only fish, and are intermediate in fishless ponds which usually contain abundant predatory chironomids (Goyke 1990). We interpret this pattern as control of chironomid densities by sculpin predation (we have proven this control in a sculpin exclusion experiment in bare sediments of Toolik Lake).

Lake trout are very effective predators on the snail Lymnaea elodes, the dominant benthic invertebrate in many arctic lakes. In lake trout lakes they restrict the snail's distribution to the lake periphery and favor Valvata on the open sediments (Hershey 1990). In these lakes, Lymnaea along the periphery are significantly smaller than in non-lake trout lakes. Thus, trout depress Lymnaea size and abundance. The effect on snails will be observed over time in the ongoing experiments where lake trout have been added to and removed from whole lakes.

Top-down effects on nutrient regeneration and storage (#32,33). We believe that there is a threshold limit for nutrient absorption; after years of eutrophication or phosphorus loading in experiments, the sediment phosphorus trap eventually breaks down and phosphorus is regenerated from the sediment under anaerobic conditions. As noted earlier, the iron-phosphorus trap worked well and no phosphorus was regenerated for a number of years in Lake N-2. For nitrogen, measurements made during the fourth year of fertilization found fluxes from the sediment to be about 1 mmol m^{-2} d^{-1}, a very high rate compared with Whalen and Cornwell's (1985) estimate of 0.05 mmol m^{-2} d^{-1} for Toolik Lake. Over a five year period in Lake N-2, the end of winter oxygenated zone shrunk by 2 m, the nitrate doubled, and the ammonium increased by 44%. Furthermore, in 1990 for the first time there was a spring bloom of algae in the lake (this occurred before the summer fertilization began). We need to duplicate this experiment and determine the threshold limit for another lake (continue to observe fertilized Lake N-1) and also observe the time Lake N-2 needs to recover from the excess nutrient loading.

STREAM RESEARCH RESULTS

Overview. An overview and synthesis of the response of the Kuparuk River biota to the addition of phosphorus is given in Fig. 10. The bottom-up effects of nutrients as they propagate through the ecosystem are diagrammed flowing from left to right. The top-down or feedback effects are diagrammed flowing from right to left. The steps are numbered and described in the following paragraph.

The sequence of responses that we have measured over the past seven years is as follows (numbers in parentheses refer to Fig. 10): Dissolved phosphate added to river water stimulates the growth of epilithic algae (1). Increases in algal production lead to sloughing and export of algal biomass and increased excretion and mortality. Increased algal excretion and mortality stimulate bacterial activity which is also stimulated directly by phosphorus addition (2, 3). Increased bacterial activity and biomass make possible an increase in the rate of decomposition of refractory compounds such as lignocellulose and many components of the DOM pool (4). The increases in algal and bacterial biomass provide increased high quality food for filtering and grazing insects (5,6). The insects respond with increased growth rate and, in the case of Baetis and Brachycentrus, with increases in density. However, Prosimulium density in the fertilized reach declines due to competitive interaction with Brachycentrus (7). The increases in insects other than Prosimulium increase the available food for grayling; both young-of-the-year and adult grayling grow faster and achieve better condition in the fertilized reach (8). In the long-term, if the experimental nutrient addition were expanded to include the whole river and barring other overriding but unknown population controls, we hypothesize that the fish population would increase (9). If so, it is possible that predation by fish would exert increased top-down control over insects such as Baetis or Brachycentrus which are vulnerable to fish predation when drifting and emerging (10). Experimental evidence from bioassays using insecticides indicates that grazing insects control algal biomass (11). Finally, increases in epilithic algae and bacteria are responsible in part for uptake of added phosphorus and ammonium and for increased uptake of naturally abundant nitrate (12). Thus, the bottom-up effects of added nutrients are paralleled by several top-down effects of fish on insects, insects on insects, insects on epilithic algae, and epilithon on dissolved nutrient levels.

In summary, the entire biological system in the river is responsive to added phosphorus. The bottom-up effects propagate to all levels in the food web. Also, both top-down effects and competitive interactions are clearly important in the response of the ecosystem to fertilization. It is also instructive to examine in more detail the accuracy of our four original predictions about how the Kuparuk River would respond to fertilization.

Prediction 1. Algal biomass and production would increase. Algal biomass increased dramatically in years 1 and 2 but only slightly in years 3, 4 and 5 (Fig. 11) in response to fertilization. Bioassays with insecticide have demonstrated that grazers are responsible for the lack of biomass response in several years (Gibeau and Miller 1989). Primary production on river bottom rocks has been stimulated by 20 to 100% by phosphorus and phosphorus plus nitrogen additions (Fig. 12).

Prediction 2. Decomposition and heterotrophic microbial activity would increase. Decomposition of fresh Carex detritus was not increased by phosphorus addition but was slightly stimulated by phosphorus plus ammonium addition. On the other hand, mineralization rates of cellulose and lignin were accelerated by phosphorus addition but decay rates were low. All measures of microbial activity including microcalorimetry (Fig. 13), acetate uptake into lipid, and decomposition of ^{14}C-labelled compounds indicated that most often the greatest activity occurred with light-grown epilithon with added phosphorus. The conclusion is that organic matter supplied by algae greatly increased heterotrophic activity in light-grown epilithon. Decomposition and heterotrophic activity did increase but mainly because of the indirect effects of algal photosynthesis.

Prediction 3. Insect growth and production would increase. This prediction was only partly correct. Growth rates of grazers (Baetis and Orthocladius) and filter feeders (Prosimulium and Brachycentrus) were frequently higher as indicated by increased size in the fertilized reach. The abundance of Brachycentrus increased in the fertilized reach but the abundance of Prosimulium declined. In years 2 and 3, total insect production was the same upstream and downstream, whereas in year 4, insect production in the fertilized reach was greater than in the control (Fig. 14). Prosimulium, which declines in abundance in the fertilized reaches, usually dominates insect production in all other reaches.

Prediction 4. Fish growth and survival would increase. Grayling growth increased for both young and adult fish (Fig. 15a,b). Production of the two most important prey of adult grayling, Baetis and Brachycentrus, was increased by the fertilization. It appears that the decline in total secondary production did not affect fish growth probably because black flies are not a regular food of the grayling. One advantage of larger size to young grayling is that burst swimming speed increases exponentially with size (Fig. 16). This means that very small increases in size can mean large increases in the ability of small grayling to resist being flushed downstream in a storm, and can increase their ability to swim upstream to find overwintering habitat. For example, a fish 30 mm in length has a swimming speed of approximately 0.15 m sec^{-1}, while a fish 37 mm in length has a sustained swimming speed of 0.4 m sec^{-1}. These differences in size are comparable to those we found in late July between the control and fertilized zones.

In summary, the four predictions were only partly correct in predicting the responses to fertilization. We did not predict the switch from control of algal biomass by nutrient supply in years 1 and 2 to control by grazers in years 3 and 4. We also did not predict the lack of response of Carex decomposition to phosphorus fertilization. We did not anticipate that heterotrophic activity of the epilithon would respond to phosphorus addition in the light but only weakly in the dark-grown community. We did not expect a decline in black fly abundance following fertilization. And it was unexpected, though understandable in retrospect, that fish growth would greatly increase in spite of little change in total insect production. Taken together, these several unexpected aspects of the response to fertilization strongly reinforce our conviction that whole-ecosystem experiments are needed to provide a basis for understanding how river ecosystems actually respond to changes in nutrient loading. Our predictions missed important aspects of the response because we were unable to anticipate several feedbacks and interactions.

Our recent findings in the Kuparuk River appear to be contrary to Hairston et al.'s (1960) theory of alternating controls. The Kuparuk system consists of three important trophic levels - the algal producers living on rocks (epilithic diatoms), the grazing and filter feeding insects, and the predatory fish. Contrary to the theory of alternations, each trophic level appears to be limited by food resources, perhaps because resources are so sparse. This is consistent with Oksanen (1988) and Schoener (1989) who found that most terrestrial exceptions to the alternating controls theory were found in areas of low productivity.

One additional point is the important interaction between the nitrogen cycle and the phosphorus cycle. Nitrate levels in the Kuparuk vary seasonally and from year to year. When phosphorus is added, nitrate can become depleted in the fertilized reach and prevent further algal accumulation. Thus the magnitude of the algal response to phosphorus addition appears to be modified by both grazer control and a secondary N limitation.

Another aspect of the study not addressed in Fig. 10 is the great year-to-year variation in the ecosystem. The general pattern of responses to fertilization pictured in Fig. 10 is consistent between zones within a year. However, the described responses of insects and fish to fertilization overlay a large year-to-year variation. For example, grayling always grow faster in the fertilized compared to the control reach, but adult grayling grow better in some years (1986, 1989) than in others (1988, 1990) in both reaches. In addition, black flies are more numerous in some years than in others. Interestingly, young-of-the-year grayling grow well in the years when adults do poorly. It appears that only by long-term study and observation will it be possible to understand the causes of these differences.

Several hypotheses can be advanced to explain this year to year variability. The variations in black fly abundance may be due to changes in discharge which may affect oviposition success and will also bring different amounts of allochthonous organic matter into the river (a food source for black flies). Also, perhaps extremely low temperatures during some winters, for example due to low snow depth, cause mortality of larvae or eggs over winter for black flies and other insects. The variations in fish growth may be related to water temperature, discharge, or to variations in food availability or combinations of factors. We record temperature and discharge and monitor insect drift each summer. Because grayling in the Kuparuk are predominantly drift feeders, over the long term we expect to see a correlation develop between growth and temperature or certain components of insect drift or both. We also plan more experimental work in stream tanks.

Preliminary work on the effectiveness of drift feeding of adult grayling has indicated a significant interaction of feeding success with current speed and debris in the water (Fig. 17). We currently have information on drift feeding in stream velocities up to 55 cm s^{-1}. Observations of grayling drift feeding in experimental stream tanks have shown that grayling search volume is reduced under high flow conditions and when plant debris is in the streamwater. We have developed a model of grayling drift feeding which indicates that larger invertebrates at moderate current speeds should be highly susceptible to fish predation. Fish are less effective predators when there is a lot of debris, such as small peat fragments, in the water. We plan to continue this work and incorporate the effects of temperature in the feeding model.

REFERENCES

Cuker, B. E. 1981. Control of epilithic community structure in an arctic lake by vertebrate predation and invertebrate grazing. Ph.D. thesis, North Carolina State University, Raleigh, 96 p.

Gibeau, G. G. and M. C. Miller. 1989. A micro-bioassay for epilithon using nutrient diffusing artificial substrata. J. of Freshwater Ecol. Vol. 5:171-176.

Goyke, A. 1990. The effects of fish predation on chironomid (Diptera:Chironomidae) community structure in arctic lakes. M.S. thesis, University of Minnesota, Duluth.

Hairston, N. G., F. E. Smith and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421-425.

Hershey, A. E. 1985. Effects of predatory sculpin on the chironomid communities in an arctic lake. Ecology 66:1131-1138.

Hershey, A. E. and A. L. Hiltner. 1988. Effects of caddisfly activity on black fly density: Interspecific interactions outweigh food limitation. Journal of the North American Benthological Society 7(3):188-196.

Hershey, A. E. and M. E. McDonald. 1985. Diet and digestion rates of slimy sculpin, *Cottus cognatus*, in an Alaskan arctic lake. Can. J. Fish. Aquat. Sci. 42:483-487.

Hobbie, J. E., T. L. Corliss, and B. J. Peterson. 1983. Seasonal patterns of bacterial abundance in an arctic lake. Arct. Alp. Res. 15:253-259.

Hobbie, J. E. and J. V. K. Helfrich III. 1988. The effect of grazing by microprotozoans on production of bacteria. Archiv. Hydrobiol. 31:281-288.

Luecke, C. and W. J. O'Brien. 1983. The effect of *Heterocope* predation on zooplankton communities in arctic ponds. Limnol. Oceanogr. 28:367-377.

McDonald, M. E., B. E. Cuker, and S. C. Mozley. 1982. Distribution, production and age structure of slimy sculpin (*Cottus cognatus*) in an arctic lake. Envir. Biol. Fish. 7:171-176.

McDonald, M. E. and A. E. Hershey. 1989. Size structure of a lake trout (*Salvelinus namaycush*) population in an Arctic lake: Influence of angling and implications for fish community structure. Can. J. Fish. Aquat. Sci. 46:2153-2156.

Miller, M. C., G. R. Hater, P. Spatt, P. Westlake, and D. Yeakel. 1986. Primary production and its control in Toolik Lake, Alaska. Arch. Hydrobiol. Suppl. 74(1):97-131.

O'Brien, W. J., C. Buchanan, and J. Haney. 1979b. Arctic zooplankton community structure: Exceptions to some general rules. Arctic 32:237-247.

Oksanen, L. 1988. Ecosystem organization: Mutualism and cybernetics or plain Darwinian struggle for existence? American Naturalist 131:424-444.

Peterson, B. J., J. E. Hobbie, and T. L. Corliss. 1986. Carbon flow in a tundra stream ecosystem. Can. J. Fish. Aquat. Sci. 43(6):1259-1270.

Schoener, T. W. 1989. Food webs from the small to the large. Ecology 70:1559-1589.

Sugimura, T. and Y. Suzuki. 1988. A high temperature catalytic oxidation method of non-volatile dissolved organic carbon in seawater by direct injection of liquid samples. Marine Chemistry 24:105-131.

Whalen, S. C. and J. C. Cornwell. 1985. Nitrogen, phosphorus and organic carbon cycling in an arctic lake. Can. J. Fish. Aquat. Sci. 42:797-808.

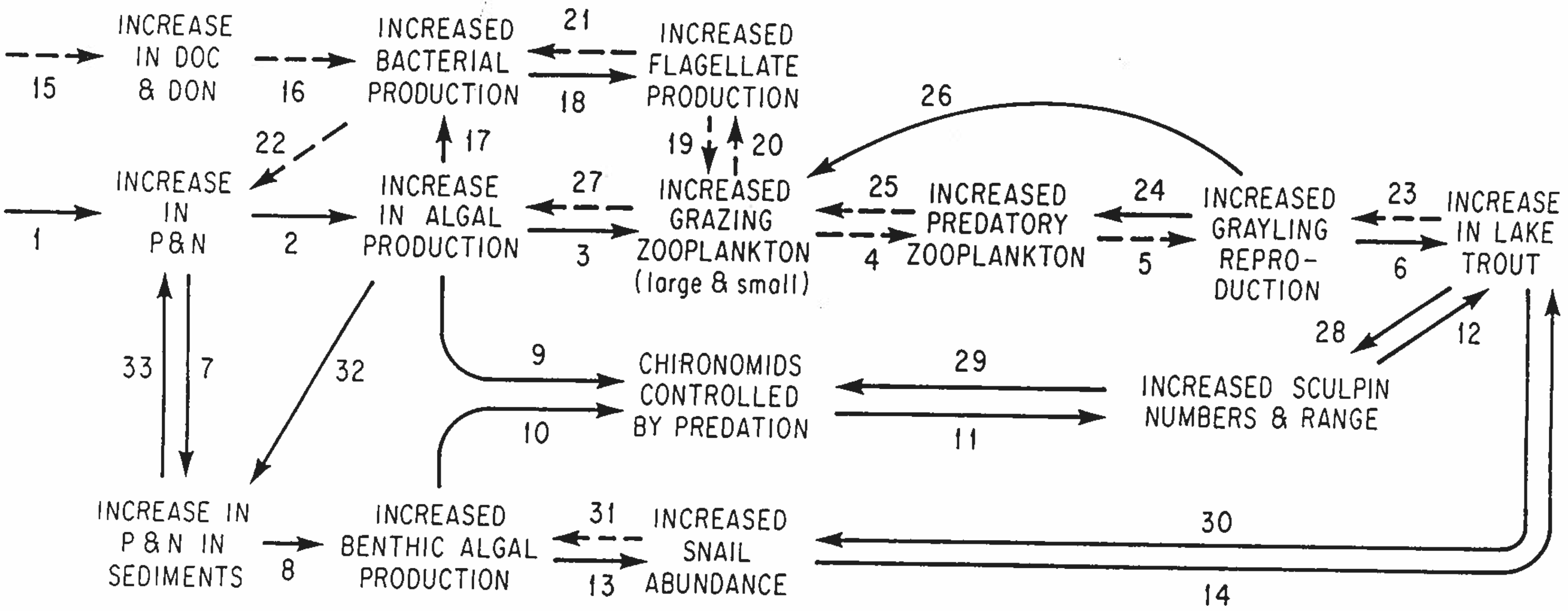


Figure *1* . Responses of the Toolik Lake ecosystem to fertilization (left-to-right arrows) and to an altered top predator (right-to-left arrows).

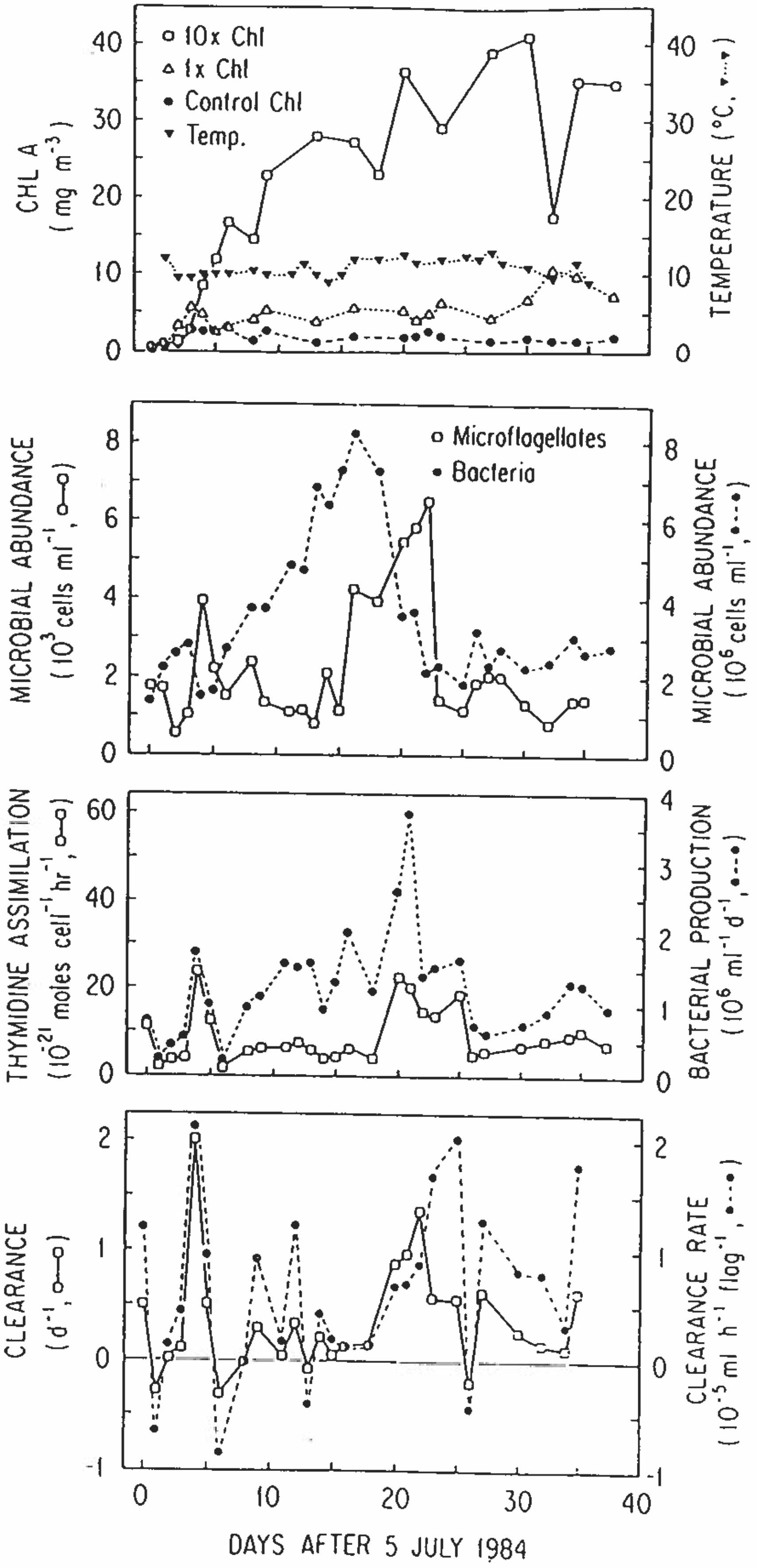


Figure 2. The concentration of chlorophyll a in limnocorrals placed in Toolik Lake in 1984. The corrals were fertilized at 1 and 10 times the rate of nutrient loading to Toolik Lake (on a square meter basis). Also shown is the bacterial and flagellate numbers, thymidine assimilation, and bacterial productivity (Hobbie and Helfrich 1988).

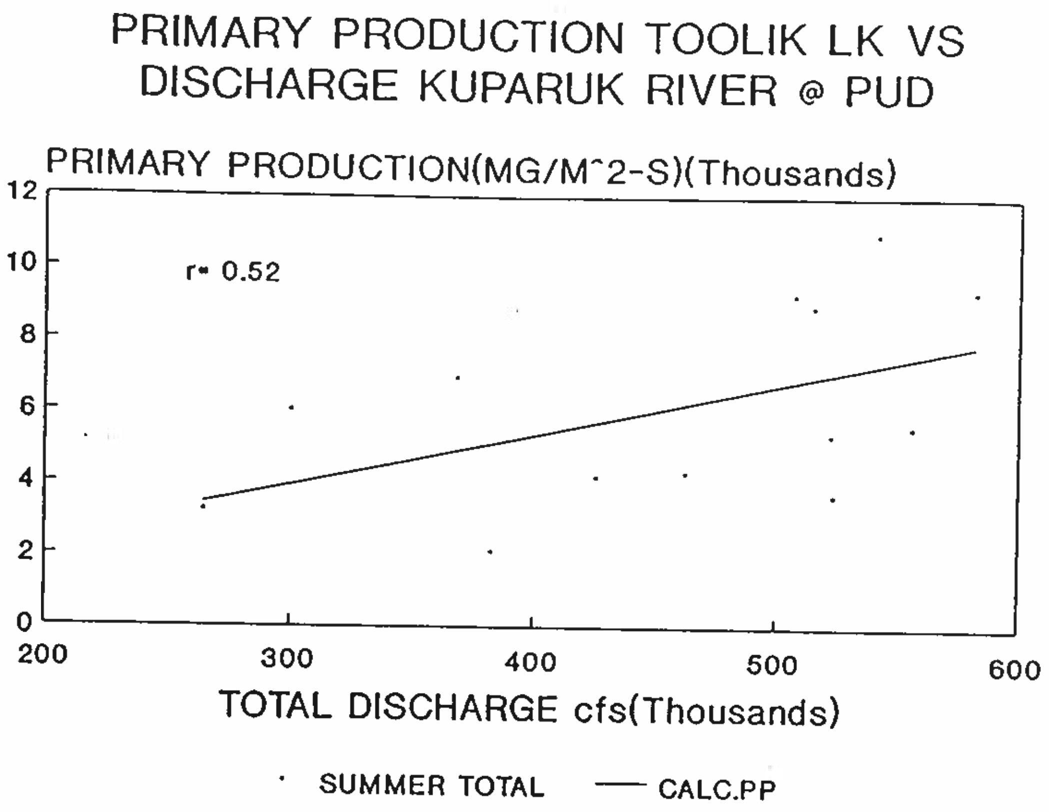


Figure 3. Long-term correlation of the total summer primary productivity of Toolik Lake with the total water flow of the near-by Kuparuk River.

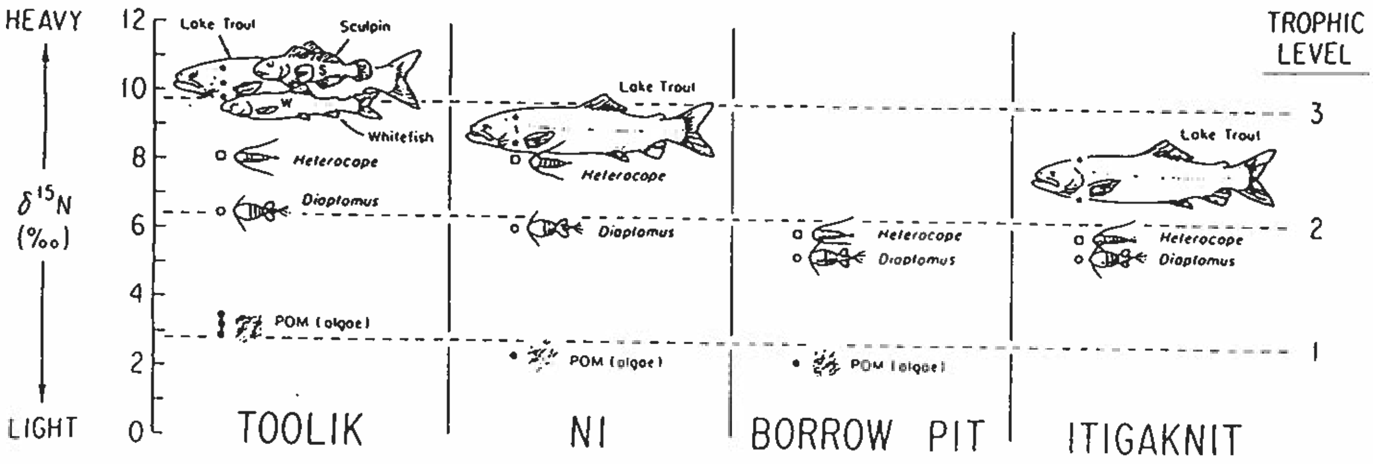


Figure 4. The delta ^{15}N of particulate organic matter (POM) from the plankton, of zooplankton, and of fish from Toolik Lake and several ponds and lakes near Toolik (Lake N-1, Itigaknit, Dam Pond). Due to an inherent physiological fractionation during protein assimilation, a predator is expected to have a delta ^{15}N value of about 3 per mil greater than its prey.

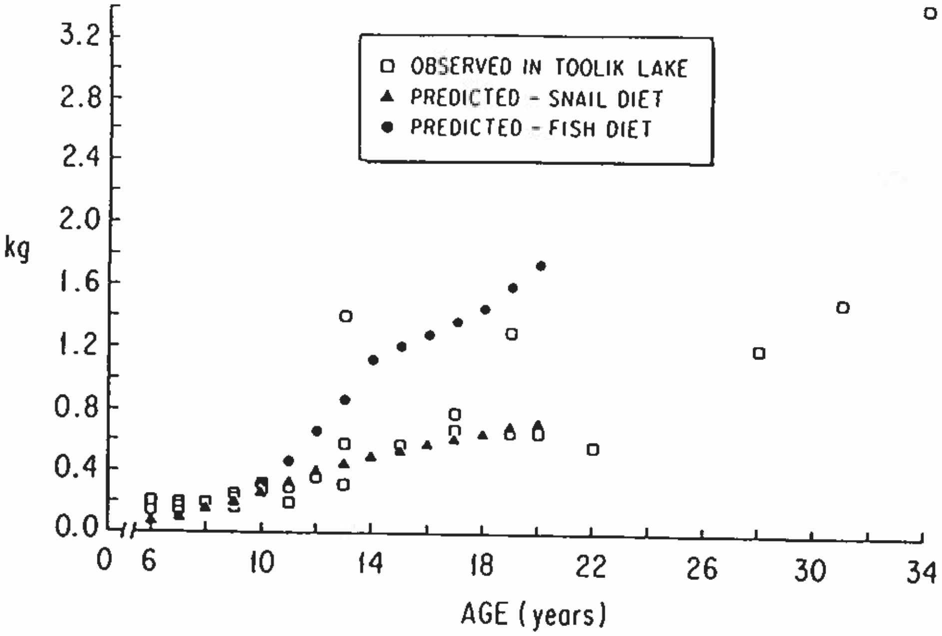


Figure 5. The weight of lake trout in Toolik Lake at various ages (squares) and the predicted weight from a bioenergetic model of lake trout growth when feeding on fish (triangles) and on snails (crosses) for the critical period from age 6 to age 20.

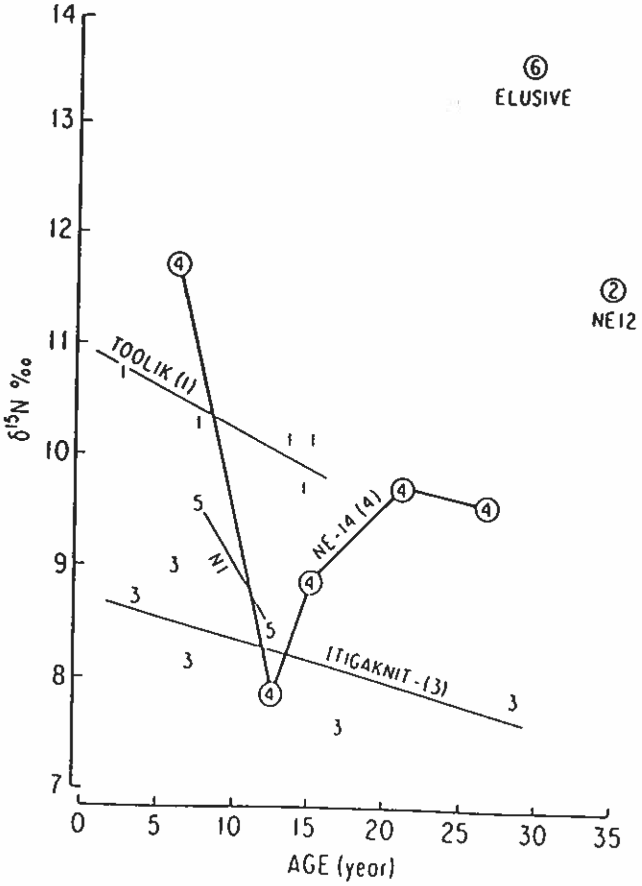
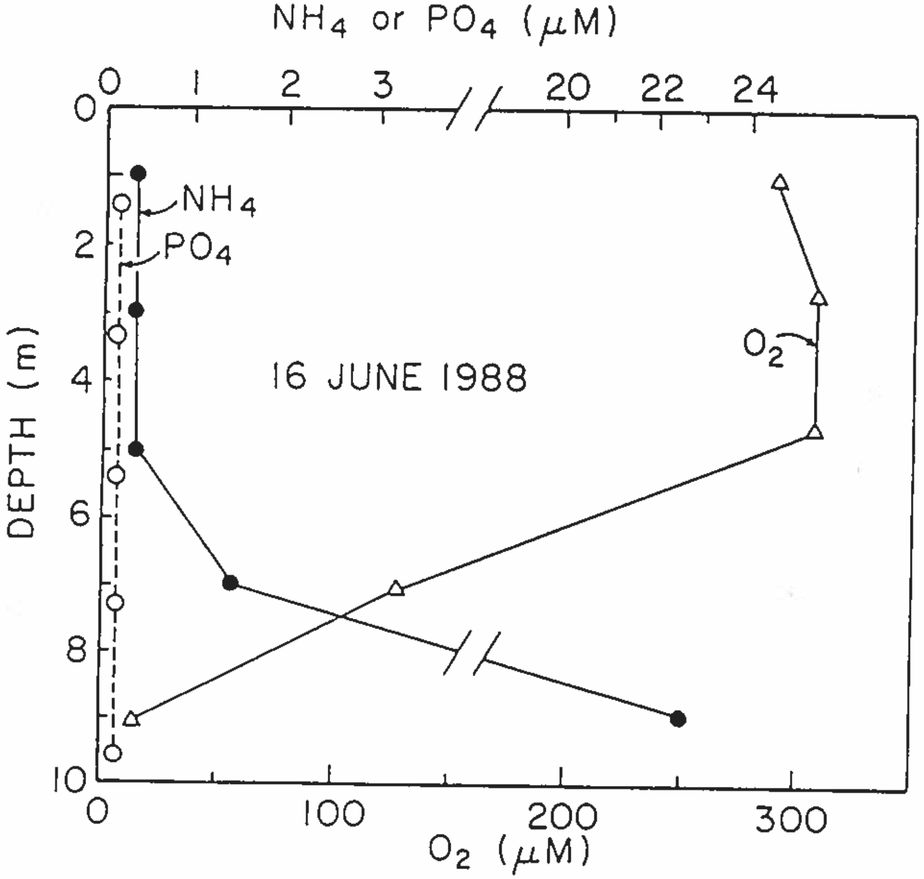


Figure 6. The delta ^{15}N of lake trout of various sizes and from various lakes in the Toolik area.



igure 7 . Spring 1988 data from Lake N-2 showing ammonia hosphate, and oxygen after the winter stratification.

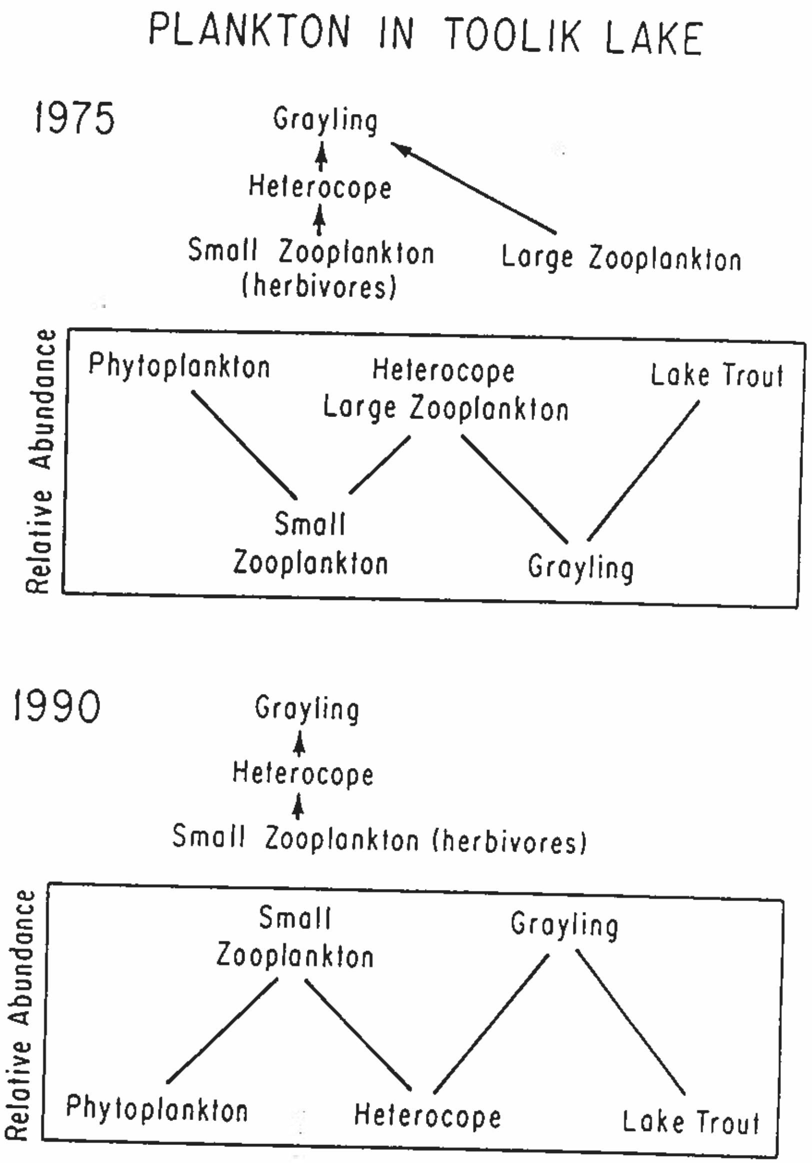


Figure 8 . Predicted feedbacks on the abundance or scarcity of animals from a lake trout reduction.

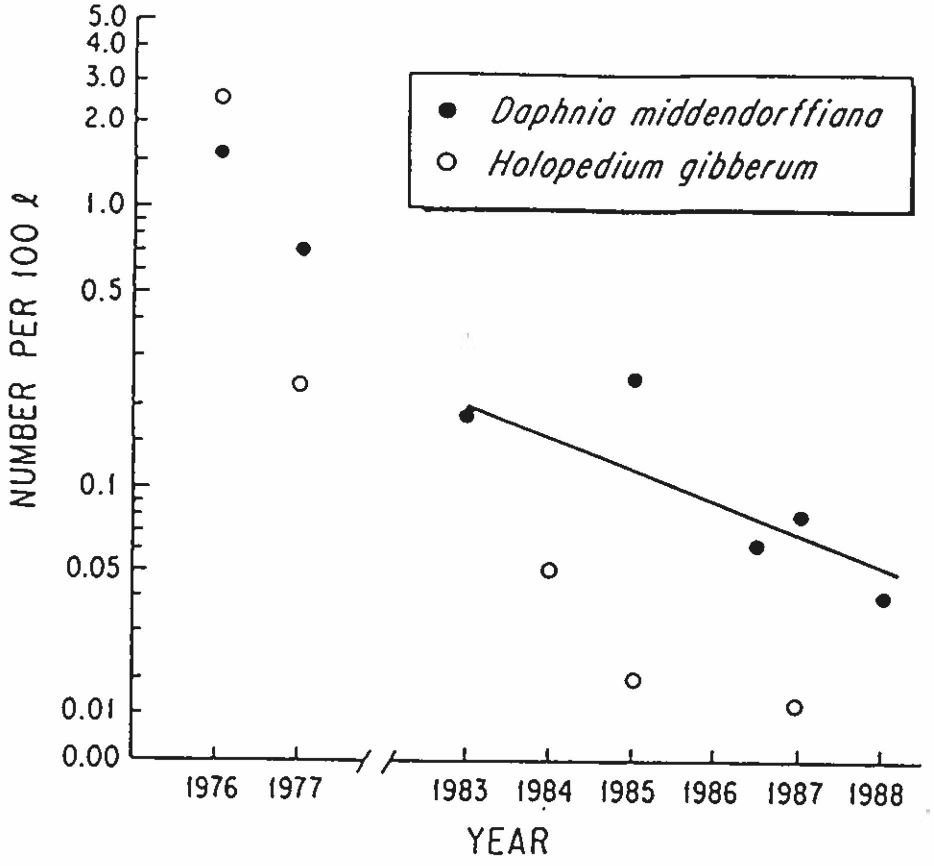


Figure 9 . Abundance of two species of large-bodied zooplankton, Daphnia middendoffiana and Holopedium gibberum, from 1975 until 1989 in Toolik Lake.

Table 1. Median fork length and weight for fish species in 1977 and 1986, Toolik Lake. Significant differences between years denoted by an asterisk. LT - lake trout, RW - round whitefish, GR - grayling.

	1986		1977		1977 min. reproductive size observed	
SPECIES	Fork length (mm)	Weight (g)	Fork length (mm)	Weight (g)	FL	WT
LT	313*	318	388	578	365	490
RW	381	680	390	760	310	300
GR	249	185	305	380	280	305

Table 2. Input rates and per cent retention for Toolik Lake (measured at lake inlet) in mmol m^{-2} yr^{-1} (Whalen and Cornwell 1985).

System	TOC (% retain)	TON (% retain)	TP (% retain)
Toolik Lake	8453 (10)	249 (18)	4.4 (30)

Table 3. Annual loading rates for nitrogen and dissolved organic carbon (DOC) in Toolik Lake. Stream inputs and outputs were measured May-August 1980. All values are as mmol m^{-2} of lake surface. Summarized from Whalen and Cornwell (1985).

	Total stream inflow	Direct precip.	Total input	Stream outflow	Net (in-out)	% input retain
Inorg. N	5.9	0.7	6.6	3.5	3.1	47
Dis. organ. N	249	2.0	251	201	50	20
Particulate N	28.4	3.6	32.0	33.4	-1.4	
Total N	283.3	6.3	290	238	52	18
DOC	8060	95	8155	7181	974	

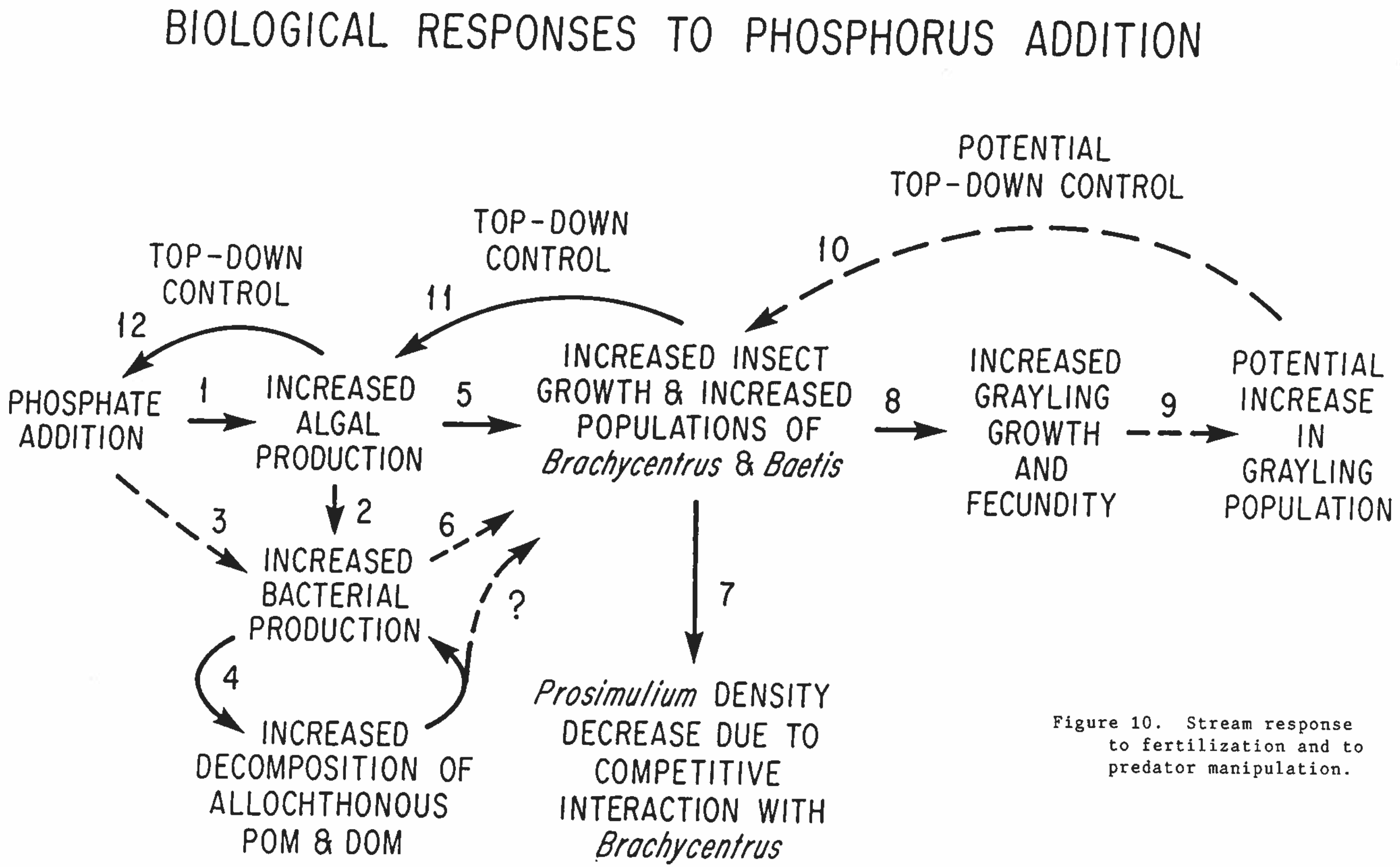


Figure 10. Stream response to fertilization and to predator manipulation.

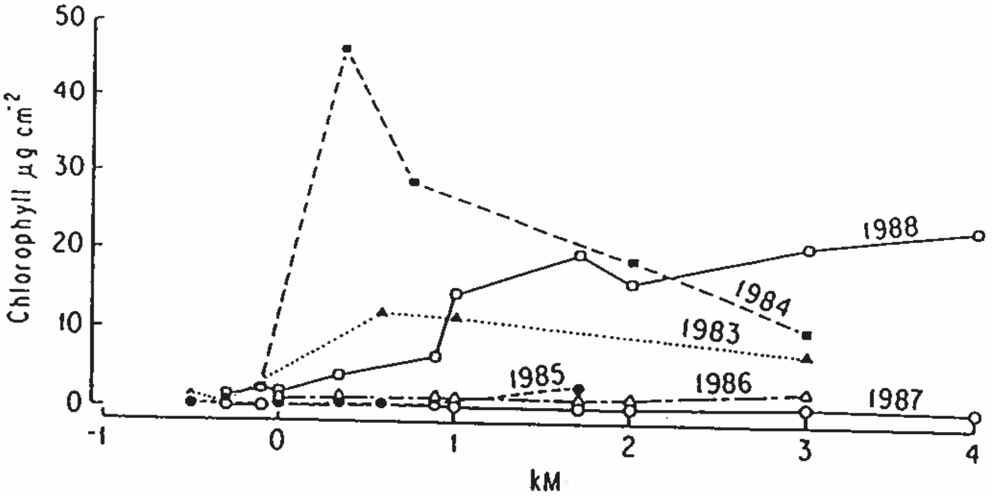


Figure 11. The total chlorophyll (µg cm-2) scrubbed from rocks in riffles of the Kuparuk River at the end of summer, 1983-1988. The rocks were located upstream (negative kilometers) or downstream (positive kilometers) from the 1983 dripper site.

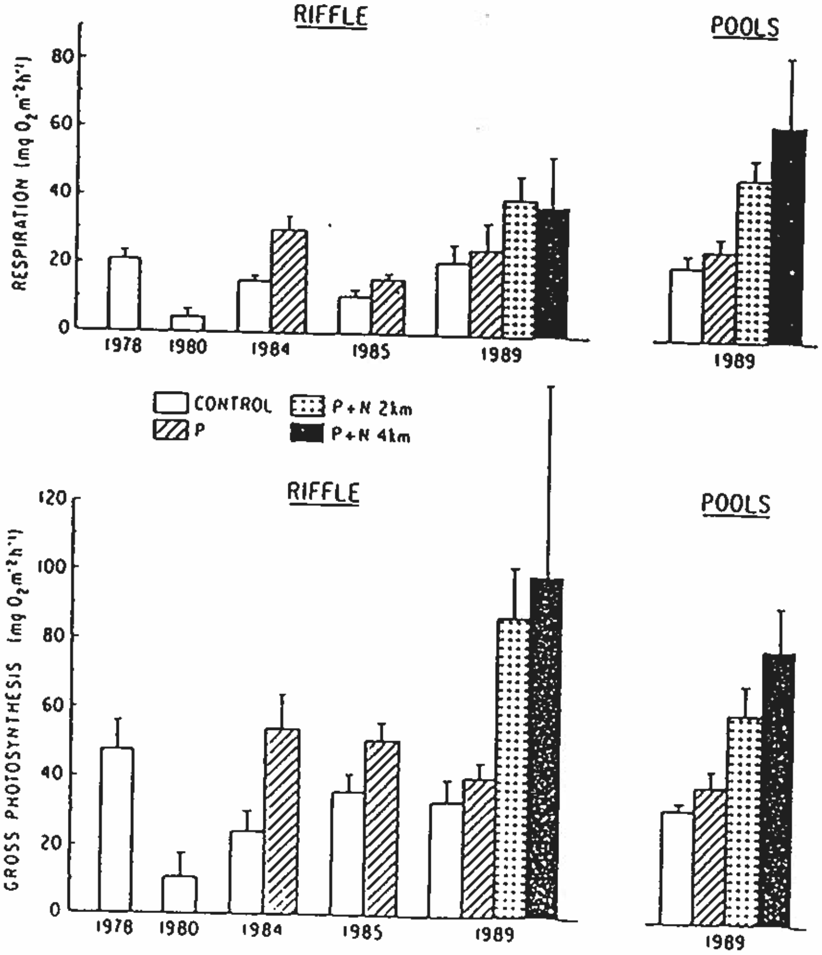


Figure 12. The mean summer gross photosynthesis and respiration (mg O_2 m^{-2} h^{-1} +/- SE) in riffles and pools of the Kuparuk River from 1978 to 1989. Samples were taken in the control reaches (upstream from nutrient addition) in the stretch fertilized with P alone, and at 2 and 4 km downstream in the stretch fertilized in 1989 with P+N.

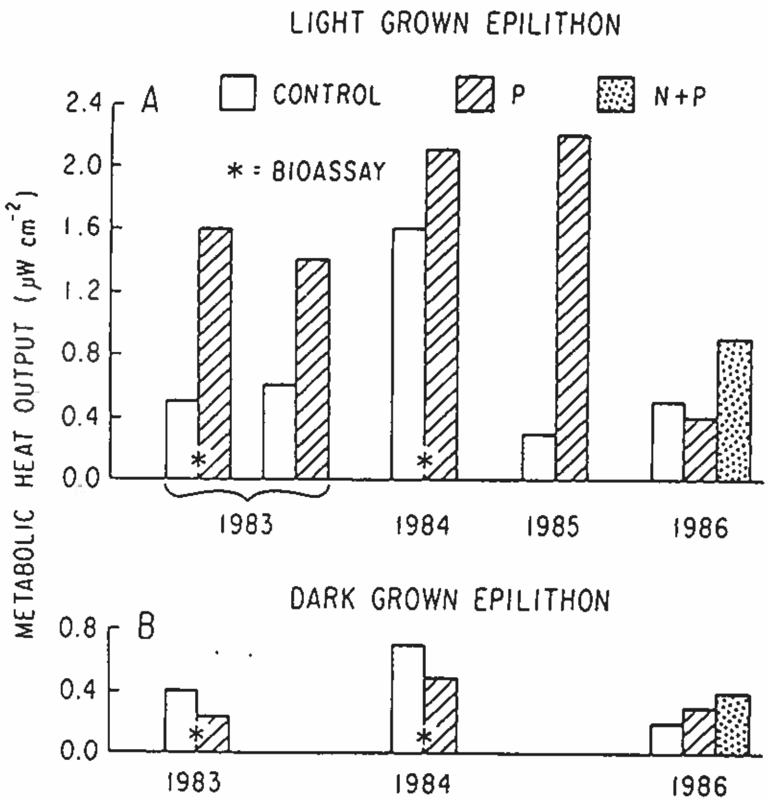


Figure /3. The output of metabolic heat, measured with a microcalorimeter, from the epilithon (biofilm) grown on glass beads (light and dark incubations) in the various experimental reaches of the Kuparuk River (data from M.Lock).

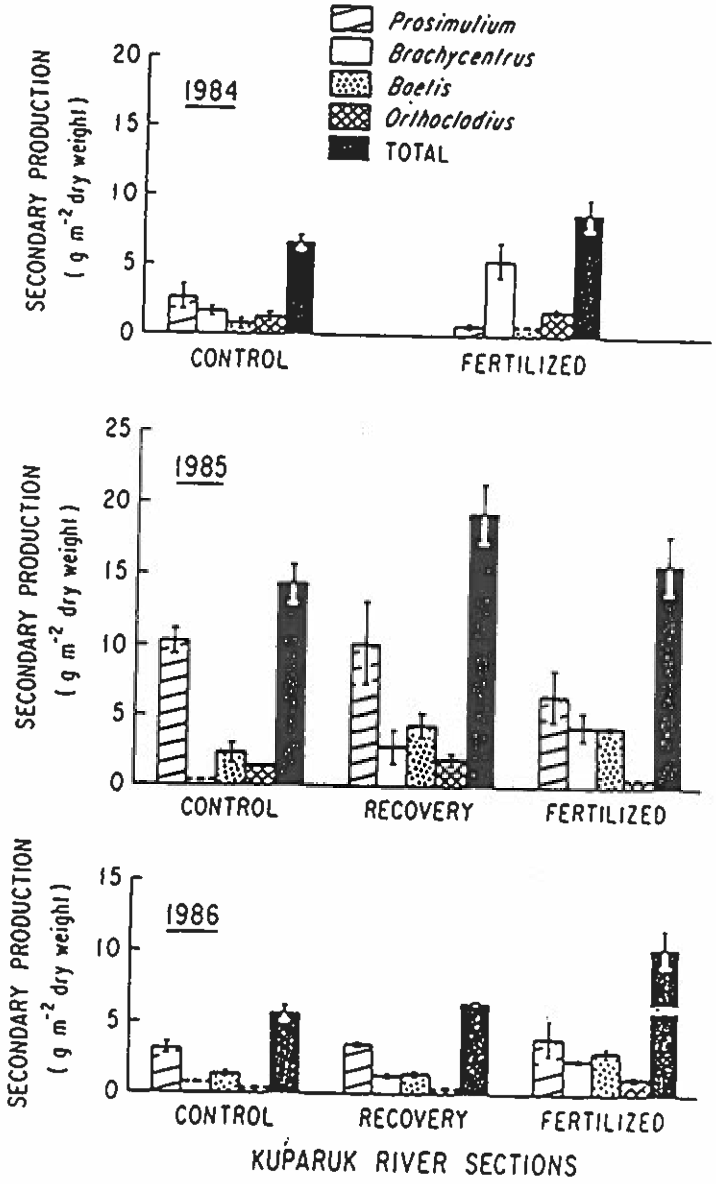


Figure /4. The production of the four dominant insects in the upstream and fertilized reaches of the Kuparuk River, 1984-1986.

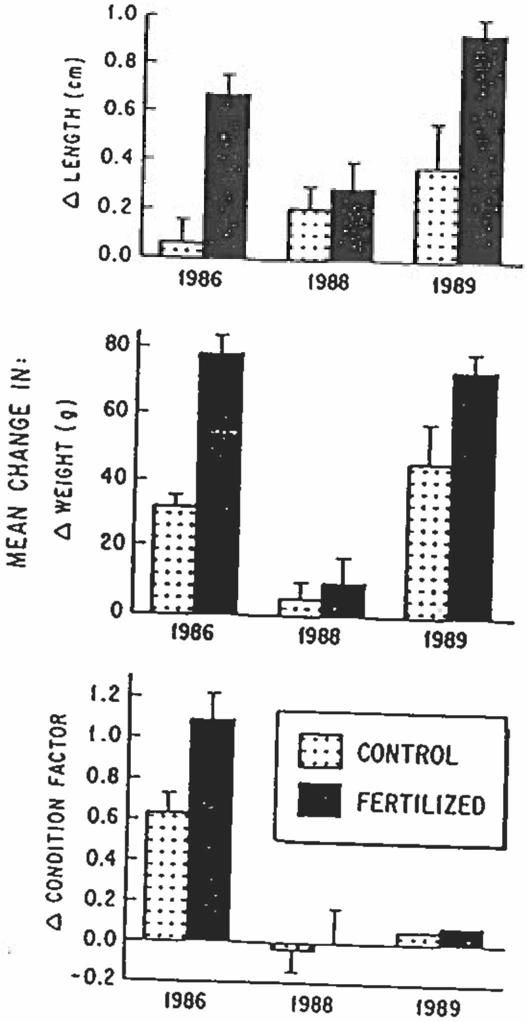
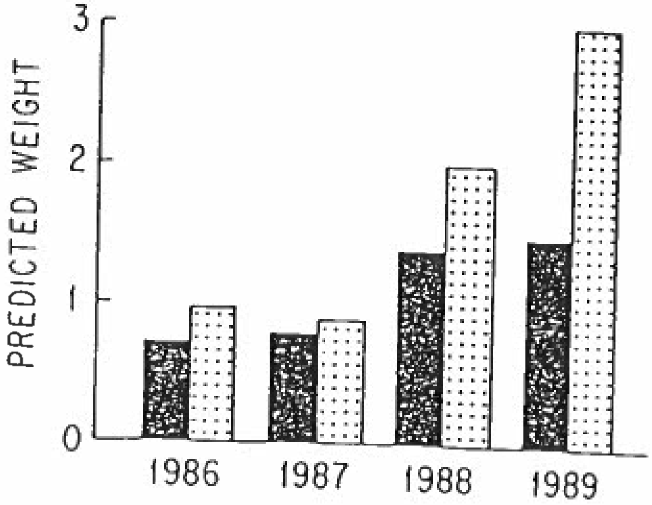


Figure 15. a. The mean changes in condition factor, weight, and length of adult grayling in various experimental reaches of the Kuparuk River, 1986, 1988, and 1989.



b. The predicted weight of young-of-the-year grayling in the Kuparuk River, 1986-1989.

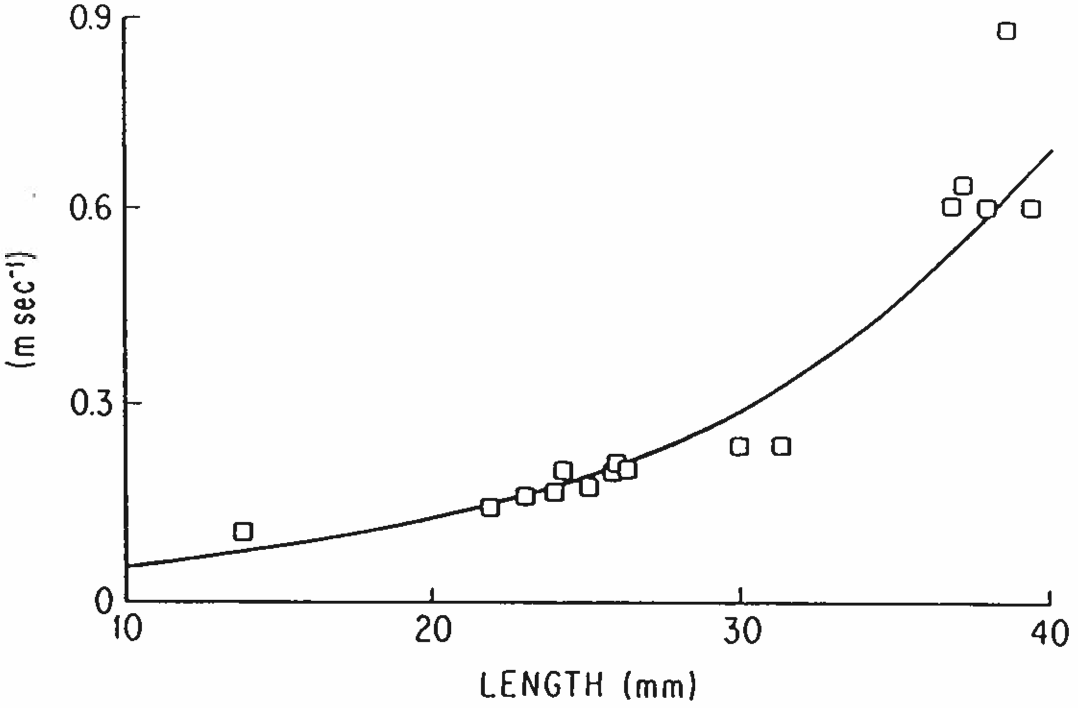


Figure 16. The burst swimming speed (m/sec) attained by Y-O-Y grayling of different sizes (millimeters of length).

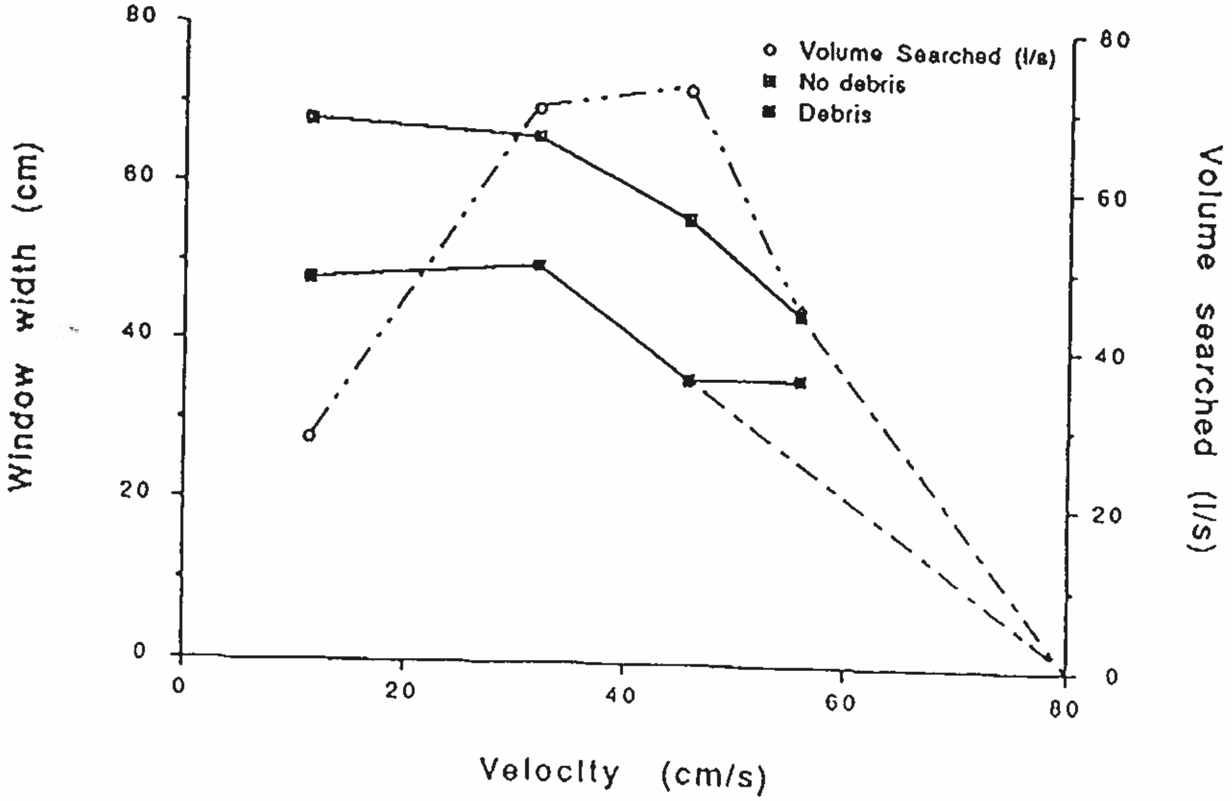


Figure 17. Width of feeding of grayling versus speed of river.

APPENDIX III

Published and Accepted Manuscripts and Theses
Aquatic Studies, Toolik Lake, Alaska
Updated June 4, 1991

Alexander, V., S. C. Whalen and K. M. Klingensmith. 1988. Nitrogen cycling in arctic lakes and ponds. Hydrobiologia 172:165-172.

Bowden, W. B., B. J. Peterson, J. C. Finlay and J. Tucker. 1991. Epilithic chlorophyll *a*, photosynthesis and respiration in control and fertilized reaches of a tundra stream. Hydrobiologia, in press.

Bowden, W. B., B. J. Peterson, J. C. Finlay and J. Tucker. (In Press). Epilithic chlorophyll a, photosynthesis, and respiration in control of a tundra stream. Hydrobiologia.

Buchanan, C. 1978. Arctic investigations of some factors that control the vertical distributions and swimming activities of zooplankton. Ph.D. thesis, University of New Hampshire. 103 p.

Buchanan, C. 1987. *Daphnia* (crustacean) swimming response to light quality in chambers simulating natural spatial distribution of light. Bull. Mar. Sci. (in press).

Buchanan, C. and J. F. Haney. 1980. Vertical migrations of zooplankton in the arctic: a test of the environmental controls. Pages 69-79 *in* W. C. Kerfoot (ed.), Evolution and ecology of zooplankton communities. The University Press of New England. Hanover, NH.

Butler, M. G. 1980. The population ecology of some arctic Alaskan Chironomidae. Ph.D. thesis, University of Michigan. 157 p.

Butler, M. G. 1982. A seven-year cycle for two *Chironomus* species in arctic Alaskan tundra ponds (Diptera: Chironomidae). Can. J. Zool. 60:58-70.

Butler, M. G. In press. Morphological and phenological delineation of *Chironomus prior* n. sp. and *C. tardus* n. sp. (Diptera: Chironomidae), sibling species from arctic Alaska. Aquatic Insects.

Cornwell, J. C. 1983. Geochemistry of Mn, Fe and P in an arctic lake. Ph.D. dissertation, University of Alaska.

Cornwell, J. C. 1985. Sediment accumulation rates in an Alaskan arctic lake using a modified ^{210}Pb technique. Can. J. Fish. Aquat. Sci. 42:809-814.

Cornwell, J. C. 1986. Diagenetic trace metal profiles in arctic lake sediments. Environmental Science Technology 20:299-302.

Cornwell, J.C.. 1987. Phosphorus cycling in arctic lake sediments: adsorption and authigenic minerals. Arch. Hydrobiol. 109:161-179.

Cornwell, J.C., 1987, Migration of metals in sediment pore waters: problems for the interpretation of historical deposition rates. In Proceedings of the 6th International Conference on Heavy Metals in the Environment Vol. 2, p.233-235, New Orleans.

Cornwell, J.C.. 1989. (in press). Manganese and iron mass balances in an arctic lake. Can. J. Fish. Aquat. Sci. (minor revision in process).

Cornwell, J. C. and G. W. Kipphut. (In Press). Biogeochemistry of manganese- and iron-rich sediments in Toolik Lake, Alaska. Hydrobiologia

Cornwell, J. C.. (In Press). Cation export from Alaskan Arctic watershed. Hydrobiologia.

Cornwell, J.C. and R.J. Barsdate, 1977, Sensitivity of arctic lakes to phosphorus loading, p. 57-61, In Technical Session Papers to the 18th Alaska Science Conference, Alaska Division of AAAS, Anchorage, Alaska.

Cornwell, J.C. and S. Banahan. (in press). A silica budget for an Alaskan arctic lake. Hydrobiologia.

Cuker, B. E. 1978. Ecology of Hydra in an arctic Alaskan lake. M.S. thesis, University of Michigan, Ann Arbor. 71 p.

Cuker, B. E. 1981. Control of epilithic community structure in an arctic lake by vertebrate predation and invertebrate grazing. Ph.D. thesis, North Carolina State University, Raleigh. 96 p.

Cuker, B. E. 1983a. Grazing and nutrient interactions in controlling the activity and composition of the epilithic algal community of an arctic lake. Limnol. Oceanogr. 28:133-141.

Cuker, B. E. 1983b. Competition and coexistence between the grazing snail Lymnaea, Chironomidae, and Microcrustacea in an arctic epilithic lacustrine community. Ecology 64:10-15.

Cuker, B. E., and S. C. Mozley. 1981. Summer population fluctuations, feeding, and growth of Hydra in an arctic lake. Limnol. Oceanogr. 26:697-708.

Cuker, B. E., M. E. McDonald and S. C. Mozley. (In Press). Size selective predation by slimy sculpin (Cottus cognatus): Its potential to alter the rocky littoral invertebrate community in an arctic lake. Hydrobiologia.

Evans, B. I. 1986. Strategies and tactics of search behavior in Salmonid and Centrarchid planktivorous fish. Ph.D. thesis, University of Kansas, Lawrence. 83 p.

Evans, B. I. and W. J. O'Brien. 1987. A re-evaluation of the search cycle of planktivorous Arctic grayling, Thymallus arcticus. Can. J. Fish. Aquat. Sci. 45:187-192.

Federle, T. W. 1981. The processes and control of the microbial colonization and decomposition of plant litter in an arctic lake. Ph.D. dissertation, Department of Biological Sciences, University of Cincinnati. 133 p.

Federle, T. W., and J. R. Vestal. 1980a. Microbial colonization and decomposition of Carex litter in an arctic lake. Appl. Environ. Microbiol. 39:888-893.

Federle, T. W., and J. R. Vestal. 1980b. Lignocellulose mineralization by arctic lake sediments in response to nutrient manipulation. Appl. Environ. Microbiol. 40:32-39.

Federle, T. W., and J. R. Vestal. 1982. Evidence of microbial succession on decaying leaf litter in an arctic lake. Can. J. Microbiol. 28:686-695.

Federle, T. W., V. L. McKinley, and J. R. Vestal. 1982. Effects of nutrient enrichment on the colonization and decomposition of plant detritus by the microbiota of an arctic lake. Can. J. Microbiol. 28:1199-1205.

Federle, T. W., V. L. McKinley, and J. R. Vestal. 1982. Physical determinants of microbial colonization and decomposition of plant litter in an arctic lake. Microbiol. Ecol. 8:127-138.

Fiebig, D. M. 1988. Riparian zone and streamwater chemistries and organic matter immobilization at the stream-bed interface. Thesis, University of Wales, Bangor, U. K. 311pp.

Ford, T. E. 1984. A study of dissolved and colloidal organic carbon in rivers and their contribution to benthic microbial metabolism. Ph.D. Thesis, University College of North Wales. 169pp.

Ford, T. E. and M. A. Lock. 1988. A microcalorimetric investigation of the effect high molecular weight organics on epilithic microbial metabolism. In Cappenberg, T. E. (ed.), Proc. 111 Int. Workshop on the Measurement of Microbial Activities in the Carbon Cycle in Aquatic Ecosystems (1984). Arch. Hydrobiol. Beih. 31:195-201.

Ford, T. E., M. Walch, R. Mitchell, M.J. Kaufman and M.A. Lock. 1989. Influence of nutrient enrichment of an arctic river on biofilm formation on metal surfaces. Biofouling, 1:301-311.

Gibeau, G. G., and M. C. Miller. 1989. A micro-bioassay for epilithon using nutrient diffusing artificial substrata. J. of Freshwater Ecol. Vol. 5:171-176.

Haney, J. and C. Buchanan. Distribution and biogeography of Daphnia in the arctic. In: R. Peters and Benito (eds.) Daphnia (in press).

Hershey, A. E. 1980. Chironomid community structure in an arctic lake: the role of a predatory chironomid . Masters Thesis. North Carolina State University, Raleigh, N. C.

Hershey, A. E. 1983. Benthic community structure in an arctic lake: fish predation foraging strategies, and prey refugia. Ph. D. Thesis North Carolina State University, Raleigh, N. C.

Hershey, A. E. 1985. Effects of predatory sculpin on the chironomid communities in an arctic lake. Ecology 66:1131-1138.

Hershey, A. E. 1985. Littoral chironomid communities in an arctic Alaskan lake. Holarctic Ecology 8:39-48.

Hershey, A. E. 1986. Selective predation by Procladius in an arctic Alaskan lake. Can. J. Fish. Aquat. Sci. 43:2523-2528.

Hershey, A. E., A. L. Hiltner, M. A. J. Hullar, M. C. Miller, R. J. Vestal, M. A. Lock, S. Rundle and B. J. Peterson. 1988. Nutrient influence on a stream grazer: Orthocladius microcommunities respond to nutrient input. Ecology 69(5) 1383-1392.

Hershey, A. E., and A. L. Hiltner. 1988. Effects of caddisfly activity on black fly density: Interspecific interactions outweigh food limitation. Journal of the North American Benthological Society 7(3): 188-196.

Hershey, A. E., and M. E. McDonald. 1985. Diet and digestion rates of slimy sculpin, Cottus cognatus, in an Alaskan arctic lake. Can. J. Fish. Aquat. Sci. 42:483-487.

Hershey, A. E.. 1989. Snail populations in arctic lakes: competition mediated by predation? Oecologia (in press)

Hiltner, A. L., and A. E. Hershey. (In Press). Black fly (Diptera: Simulidae) responses to phosphorus enrichment of an arctic tundra stream. Hydrobiologia.

Hiltner, A. L.. 1985. Response of two black fly species (Diptera: Simuliidae to phosphorus enrichment of an arctic tundra stream. M. S. Thesis, University of Wisconsin, Madison, Wisconsin.

Hinterleitner-Anderson, D. and A. E. Hershey. (In Press). The effects of river fertilization of Mayfly (Baetis sp.) drift patterns and population density in an arctic river. (Hydrobiologia).

Hobbie, J. E. 1983. Polar limnology. In: F. B. Taub (ed.), Lakes and reservoirs. Elsevier Scientific Publishing Co., Amsterdam, Netherlands.

Hobbie, J. E. and J. V. K. Helfrich III. 1988. The effect of grazing by microprotozoans on production of bacteria. Archiv. Hydrobiol. Beih. 31:281-288.

Hobbie, J. E., B. J. Peterson, G. R. Shaver and W. J. O'Brien. In press. The Toolik Lake Project: A terrestrial and freshwater program for global change. Proceedings of a University of Alaska Symposium on Global Change in the Arctic.

Hobbie, J. E., T. L. Corliss, and B. J. Peterson. 1983. Seasonal patterns of bacterial abundance in an arctic lake. Arct. Alp. Res. 15:253-259.

Hobbie, J. E.. 1984. The ecology of tundra ponds of the Arctic Coastal Plain: a community profile. U. S. Fish and Wildlife Service FWS/OBS-83/25. 52 pp.

Hobbie, J. E.. (ed.) 1980. Limnology of tundra ponds: Barrow, Alaska. Dowden, Hutchinson and Ross, Stroudsburg, Pa. 514p.

Hullar, M. A. J. 1986 The effects of nutrient enrichment and light regimes on the epilithic microbiota of an oligotrophic arctic river. M. S. Thesis, Univ. of Cincinnati. 100 pp.

Hullar, M. A. and J. R. Vestal. 1989. The effects of nutrient limitation and stream discharge on the epilithic microbial community in an arctic stream. Hydrobiol. 172:19-26.

Hullar, M. A. J., M. J. Kaufman and J. R. Vestal. 1986. The effects of nutrient enrichment on the distribution of microbial heterotrophic activity in Arctic lakes. IN: F. Megusar and M. Gantar (eds.) Perspectives in Microbial Ecology, Slonere Society for Microbiology, Ljublja.

Johnston, C. J. 1986. Microbially mediated Mn(II) oxidation in an oligotrophic arctic lake. M.S. Thesis, University of Alaska-Fairbanks. 71 pp.

Johnston, C. J., and G. W. Kipphut. 1988. Microbially mediated Mn(II) oxidation in an oligotrophic arctic lake. Applied and Environmental Microbiology 54:1440-1445.

Jordan, M. J., J. E. Hobbie, and B. J. Peterson. 1978. Effect of petroleum hydrocarbons on microbial populations in an arctic lake. Arctic 31:170-179.

Kettle, D., and W. J. O'Brien. 1978. Vulnerability of arctic zooplankton to lake trout predation. J. Fish. Res. Bd. Can. 35:1495-1500.

Kipphut, G. W.. 1988. Sediments and organic carbon in an arctic lake. In: E. T. Degens, S. Kempe, and A. S. Naidu (eds.), Transport of Carbon and Minerals in Major World Rivers, Lakes and Estuaries, Pt. 5. Mitt. Geol. Peleont. Inst. Univ. Hamburg, Vol 66. SCOPE/UNEP, Hamburg, FRG.

Kipphut, G. W. and S. C. Whalen. (In Press). Access pipes for sampling through thick ice. (Hydrobiologia).

Kling, G. W., G. W. Kipphut, and M. C. Miller. 1991. Arctic lakes and rivers as gas conduits to the atmosphere: implications for tundra carbon budgets. Science 251:298-301.

Kling, G. W., B. Fry, & W. J. O'Brien. In press. Stable isotopes and planktonic trophic structure in arctic lakes. Ecology.

Kling, G. W., G. W. Kipphut, & M. C. Miller. In press. The flux of carbon dioxide and methane from lakes and rivers in arctic Alaska. Hydrobiologia.

Kling, G. W., W. J. O'Brien, M. C. Miller, and A. E. Hershey. In press. A biogeochemical survey of lakes and rivers on the North Slope of Alaska. Hydrobiologia.

Klingensmith, K. M. 1981. Sediment nitrification, denitrification, and nitrous oxide production in an arctic lake. M.S. thesis, University of Alaska.

Klingensmith, K. M., and V. Alexander. 1983. Sediment nitrification, denitrification and nitrous oxide production in a deep arctic lake. Appl. Environ. Microbiol. 46:1084-1092.

Kriet, K., B. J. Peterson and T. L. Corliss. In press. Water and sediment export of the Upper Kuparuk drainage of the North Slope of Alaska. Hydrobiologia.

Lock, M.A. and T.E. Ford. 1986. Colloidal and dissolved organic carbon dynamics in undisturbed boreal forest catchments. A seasonal study of apparent molecular weight spectra. Freshwat. Biol. 16: 187-195.

Lock, M.A. and T.E. Ford. 1988. Metabolism of dissolved organic matter by attached microorganisms in rivers. Proc. 1V ISME (1984) 367-374.

Lock, M.A., T.E. Ford and M.C. Miller. In press. Photolysis - a significant intermediary in carbon flow in an arctic river.

Lock, M.A., T.E. Ford, D.M. Fiebig, M.C. Miller, M. Hullar, J.R. Vestal, B.J. Peterson and J.E. Hobbie. 1989. A biogeochemical survey of rivers and streams in the mountains and foot-hills province of arctic Alaska. Arch. Hydrobiol. 115:499-521.

Lock, M.A., T.E. Ford, M. Hullar, M. Kaufman, J.R. Vestal, G.S. Volk and R.M. Ventullo. In press. Phosphorus limitation in an arctic river biofilm - a whole ecosystem experiment.

Luecke, C. 1981. The effect of Heterocope predation on arctic pond zooplankton communities. M.A. thesis, University of Kansas.

Luecke, C., and W. J. O'Brien. 1981. Phototoxicity of arctic zooplankton: Selective factors in color morphs in Heterocope. Limnol. Oceanogr. 26:454-460.

Luecke, C., and W. J. O'Brien. 1983. Photoprotective pigments in a pond morph of Daphnia middendorffiana. Arctic 36:365-368.

Luecke, C., and W. J. O'Brien. 1983. The effect of Heterocope predation on zooplankton communities in arctic ponds. Limnol. Oceanogr. 28:367-377.

Luecke, C., and W. J. O'Brien. (In Press). Photoprotective pigmentation of freshwater zooplankton: A phenomenon of extreme environments. Adaptive coloration in Invertebrates. Proceedings of a Symposium sponsored by the American Society of Zoologists, pp. 101-108.

McDonald, M. E. and A. E. Hershey. 1989. Size structure of a lake trout (Salvelinus namaycush) population in an Arctic lake: influence of angling and implications for fish community structure. Can. J. Fish. Aquat. Sci. 46:2153-2156.

McDonald, M. E. and A. E. Hershey. (In Press). Shifts in abundance and growth of slimy sculpin in response to changes in the predator population in an arctic Alaska lake. (Hydrobiologia).

McDonald, M. E., A. E. Hershey and W. J. O'Brien. (In Press). Cost of predation avoidance in young-of-year lake trout (Salvelinus namaycush): Growth differential in sub-optimal habitats. (Hydrobiologia).

McDonald, M. E., B. E. Cuker, and S. C. Mozley. 1982. Distribution, production and age structure of slimy sculpin (Cottus cognatus) in an arctic lake. Envir. Biol. Fish. 7:171-176.

McKinley, V. L., and J. R. Vestal. 1982. The effects of acid on plant litter decomposition in an arctic lake. Appl. Environ. Microbiol. 43:1188-1195.

McKinley, V. L., T. W. Federle, and J. R. Vestal. 1982. Effects of petroleum hydrocarbons on plant litter microbiota in an arctic lake. Appl. Environ. Microbiol. 43:129-135.

McKinley, V. L., T. W. Federle, and J. R. Vestal. 1983. Improvements in and environmental applications of double vial radiorespirometry for the study of microbial mineralization. Appl. Environ. Microbiol. 45:255-259.

Meininger, C. A. (in press). Differences in the Tardigrada (water bears) living in the submerged and emergent mosses from a lake, pond, and ephemeral pool of the Alaskan tundra.

Merrick, G. E. 1989. Lake trout (Salvelinus namaycush) and benthic community ecology in an arctic ecosystem. M. S. Thesis, University of Minnesota-Duluth, Duluth, Minnesota.

Merrick, G. W., A. E. Hershey and M. E. McDonald. 1991. Lake Trout (Salvelinus namaycush) control of snail density and size distribution in an arctic lake. Can. J. Fish. Aquat. Sci. 48: .

Merrick, G. W., A. E. Hershey and M. E. McDonald. (In Press). Salmon diet and the size, distribution, and density of benthic invertebrates in an arctic lake. (Hydrobiologia).

Miller, M. C. and J. E. Hobbie. 1976. R.A.T.E.--The Toolik Lake Program. Arctic Bull. 2:161-164.

Miller, M. C. and J. P. Reed. 1975. Benthic metabolism of arctic coastal ponds, Barrow, Alaska. Ver. Int. Verein. Limnol. 19:459-465.

Miller, M. C., G. R. Hater and J. R. Vestal. 1978. Effects of Prudhoe crude oil on carbon assimilation by planktonic algae in an arctic pond. pp 833-850. IN: Adriano, D. D. and I. L. Brisbin, (eds.) Environmental Chemistry and Cycling Processes. U. S. Dept. of Energy. CONF760429.

Miller, M. C., G. R. Hater, P. Spatt, P. Westlake, and D. Yeakel. 1986. Primary production and its control in Toolik Lake, Alaska. Arch. Hydrobiol. Suppl. 74(1):97-131.

Miller, M. C., J. R. Stout and V. Alexander. 1986. Effects of a Controlled Under-ice Oil Spill on Invertebrates of an Arctic and a Subarctic Stream. Environmental Pollution 42:99-132.

Miller, M. C., J. R. Vestal, S. Mozley, M. Butler, And J. E. Hobbie. 1977. Effects of Prudhoe crude oil on coastal tundra ponds. pp 521-529. IN: Energy/Environment II. USEPA Decision Series EPA600/977012.

Miller, M. C., V. Alexander and R. J. Barsdate. 1978. The effects of oil spills on phytoplankton in an arctic lake and ponds. Arctic 3:192-218.

Miller, M. C. and J. R. Stout. 1989. Variability of macroinvertebrate community composition in an arctic and subarctic stream. pp 111-128 IN: Vincent, W. F. and J. C. Ellis-Evans. High latitude Limnology. Kluwer Academic Publ., Dordrecht, Netherlands.

Miller, M. C., and J. R. Stout. 1989. Variability of macroinvertebrate community composition in an arctic and subarctic stream. Hydrobiol. 172:111-127.

Miller, M. C., and P. deOliveira. (In Press). Epilithic diatom community response to 4 years of PO4 fertiliation: Kuparuk River, Alaska. (Hydrobiologia).

Mozley, S. C. 1979. Neglected characters in larval morphology as tools in taxonomy and phylogeny of Chironomidae. Ent. Scand. Suppl. 10:27-36.

Mozley, S. C. and B. E. Cuker. (In Press). Benthic animal distributions among Alaskan north slope lakes. (Hydrobiologia).

O'Brien, W. J. 1988. The effect of container size on the feeding rate of Heterocope septentrionalis: A freshwater predaceous copepod. J. Plankton Res. 10:313-317.

O'Brien, W. J. and B. I. Evans. (In Press). Saltatory search behavior in five species of planktivorous fish. Verh. Int. Verein. Limnol.

O'Brien, W. J. and C. Luecke. 1988. The coexistence of a predaceous copeopod and a daphnid: Weeding in the Arctic. Int. Ver. Limnol. Verh. Limnol. 23:2069-2074.

O'Brien, W. J., A. Hershey, M. A. J. Hullar, J. Hobbie, G. Kipphut, M. Miller, B. Moller, and R. Vestal. Regulation of arctic lake ecosystems: A limnocorral experiment. (Hydrobiologia - submitted).

O'Brien, W. J., and B. I. Evans. (In Press). Simulation model of the planktivorous feeding of arctic grayling: Laboratory and field verification. (Hydrobiologia).

O'Brien, W. J., and D. Kettle. 1981. A zooplankton bioassay chamber for lab and field use. Jour. Plank. Res. 3:561-566.

O'Brien, W. J., and D. Schmidt. 1979. Arctic Bosmina morphology and copepod predation. Limnol. Oceanogr. 24:564-568.

O'Brien, W. J., C. Buchanan, and J. Haney. 1979b. Arctic zooplankton community structure: Exceptions to some general rules. Arctic 32:237-247.

O'Brien, W. J., D. Kettle, and H. Riessen. 1979. Helmets and invisible armor: Structures reducing predation from tactile and visual planktivores. Ecology 60:287-294.

O'Brien, W. J., H. I. Browman and B. I. Evans. 1990. Search strategies for foraging animals. American Scientist.

O'Brien, W. J., H. Riessen, D. Schmidt, D. Kettle, and D. Wright. 1980. Dimorphic Daphnia longiremis: Predator and competitive interactions. Pages 497-505. In: W. C. Kerfoot (ed.), Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.

Peterson, B. J., J. E. Hobbie, A. E. Hershey, M. A. Lock, T. E. Ford, J. R. Vestal, V. L. McKinley, M. A. J. Hullar, M. C. Miller, R. M. Ventullo, and G. S. Volk. 1985. Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. Science 229:1383-1386.

Peterson, B. J., J. E. Hobbie, and J. F. Haney. 1978. Daphnia grazing on natural bacteria. Limnol Oceanogr. 23:1039-1044.

Peterson, B. J., J. E. Hobbie, and T. L. Corliss. 1986. Carbon flow in a tundra stream ecosystem. Can. J. Fish. Aquat. Sci.

Peterson, B. J., J. E. Hobbie, T. L. Corliss, and K. Kriet. 1983. A continuous-flow periphyton bioassay: Tests of nutrient limitation in a tundra stream. Limnol. Oceanogr. 28:583-591.

Peterson, B. J., T. L. Corliss, K. Kriet and J. E. Hobbie. 1991. Nitrogen and phosphorus concentration and export for the Upper Kuparuk River on the North Slope of Alaska in 1980. Hydrobiologia, in press.

Riessen, H., and W. J. O'Brien. 1980. Re-evaluation of the taxonomy of Daphnia longiremis Sars, 1862 (Crustacea:Cladocera): Description of a new morph from Alaska. Crustaceana 38:1-11.

Rublee, P. A.. (In Press). Observations on microplankton in the Toolik Lakes. (Hydrobiologia).

Schmidt, D. R. 1980. The planktivorous feeding ecology of arctic grayling (Thymallus arcticus). M.A. thesis, University of Kansas.

Schmidt, D., and W. J. O'Brien. 1982. Planktivorous feeding ecology of arctic grayling (Thymallus arcticus). Can. J. Fish. Aquat. Sci. 39:475-482.

Showalter, J. and J. O'Brien. Measurement and model of drift feeding in Arctic Grayling. (Can. J. Fish. Sci. - submitted).

Skvorc, P. 1980. Toxic effects of Prudhoe Bay crude oil on arctic freshwater zooplankton. M.S. thesis, University of Kansas.

Sommer, M. E. 1979. Role of zooplankton grazers in determining composition and productivity of seston in arctic lakes and ponds. M.S. thesis, University of Cincinnati.

Spatt, P. D. and M. C. Miller. 1981. Growth Conditions and Vitality of Sphagnum tundra Community along the Alaska Pipeline Haul Road. Arctic 34:48-54.

Sugai, S. F. and G. W Kipphut. In press. Influence of light upon the sediment chemistry of iron in an arctic lake. (Hydrobiologia).

Whalen, S. C.. 1986. Pelagic nitrogen cycles in an arctic lake. Ph. D. Thesis, Oceanography, Univ of Alaska, Fairbanks.

Whalen, S. C., and V. Alexander. 1984a. Diel variations in inorganic carbon and nitrogen uptake by phytoplankton in an arctic lake. Journal of Plankton Research 6(4):571-590.

Whalen, S. C., and V. Alexander. 1984b. Influence of temperature and light on rates of inorganic nitrogen transport by algae in an arctic lake. Can. J. Fish. Aq. Sci. 41(9):1310-1318.

Whalen, S. C. and V. Alexander. 1986. Seasonal inorganic carbon and nitrogen transport by phytoplankton in an arctic lake. Can. J. Fish Aquat. Sci. 43:1177-1186.

Whalen, S. C. and V. Alexander. 1986. Chemical influences on ^{14}C and ^{15}C primary production in an arctic lake. Polar Biology 5:211-219.

Whalen, S. C., and J. C. Cornwell. 1985. Nitrogen, phosphorus and organic carbon cycling in an arctic lake. Can. J. Fish. Aquat. Sci. 42:797-808.

Whalen, S. C., J. C. Cornwell and V. Alexander. 1988. Comparison of chemical and biological N budgets in an Arctic lake: Implications for phytoplankton production. p. 99-115. Mitt. Geol. Paleont. Inst. Univ. Hamburg. SCOPE/UNEP Sonderbd. 66:99-115.

Wulker, W. F., and M. G. Butler. In press. Karyosystematics and morphology of northern *Chironomus* (Diptera:Chironomidae): Freshwater species with larvae of the salinarius - type. Ent. Scand.

Yeakel, D. 1978. Primary production of epilithic periphyton in a deep arctic lake. M.S. thesis, University of Cincinnati.

Manuscripts Submitted to Special Issue of Hydrobiologia.

Bowden, W. B., B. J. Peterson, J. C. Finlay and J. Tucker. Epilithic chlorophyll *a*, photosynthesis and respiration in control and fertilized reaches of a tundra stream.

Gibeau, G. G., M. C. Miller and A. E. Hershey. Invertebrate grazing impact of periphyton in a P-fertilized arctic river

Hinterleitner-Anderson, D. and A. Hershey. The effects of river fertilization on mayfly (*Baetis* sp.) drift patterns and population density in an arctic river.

Kipphut, G. W. and J. C. Cornwell. Spatial variety of chemical processes within an arctic basin.

Kling, G. W., M. C. Miller, W. J. O'Brien, and A. E. Hershey. Biogeochemical survey of lakes on the North Slope of Alaska.

Kling, G. W., G. W. Kipphut, M. C. Miller. CO_2 and methane flux in aquatic systems of Arctic Alaska.

Kriet, K., B. J. Peterson and T. L. Corliss. Hydrology and sediment transport of the upper Kuparuk River drainage of the North Slope of Alaska.

McDonald, M. E. and A. E. Hershey. Shifts in abundance and growth of slimy sculpin in response to changes in the predator population in an arctic Alaska lake.

McDonald, M. E., A. E. Hershey and W. J. O'Brien. Cost of predation avoidance in young-of-the-year lake trout (*Salvelinus namaycush*): Growth differential in sub-optimal habitats.

Merrick, G. W., A. E. Hershey and M. E. McDonald. Salmonid diet and the size, distribution and density of benthic invertebrates in an arctic lake.

Miller M. C. and B. Moller. DCMU induced fluorescence: An evaluation of its use in detecting periphyton condition in lakes of known nutrient history

O'Brien, W. J. and B. I. Evans. Simulation model of the planktivorous feeding of arctic graYling: Laboratory and field verification.

O'Brien, W. J., A. E. Hershey, J. E. Hobbie, M. A. Hullar, G. W. Kipphut, M. C. Miller, B. Moller and J. R. Vestal. Control mechanisms of arctic lake ecosystems: A limnocorral experiment.

Peterson, B. J., T. Corliss, K. Kriet and J. E. Hobbie. Nitrogen and phosphorus concentration and export for an Alaskan tundra stream

watershed.

Rublee, P. A. Observations on microplankton in the Toolik Lakes.

APPENDIX III (continued)

Published and Accepted Manuscripts and Theses
Terrestrial Studies, Toolik Lake, Alaska
Updated June 4, 1991

Note: For completeness, most of the work carried out in the Toolik area is included. Those manuscripts not associated with current LTER investigators are denoted with an asterisk.

*Batzli, G. O., and H. Henttonen. 1990. Demography and resource use by microtine rodents near Toolik Lake, Alaska. Arctic and Alpine Research 22:51-64.

*Bishop, S. C., and F. S. Chapin, III. 1989. Establishment of Salix alaxensis on a gravel pad in arctic Alaska. J. Appl. Ecol. 26:575-583.

*Bishop, S. C., and F. S. Chapin, III. 1989. Patterns of natural revegetation on abandoned gravel pads in arctic Alaska. J. Appl. Ecol. 26:1073-1082.

*Cargill, S., and F. S. Chapin, III. 1987. Application of successional theory to problems of ecosystem restoration in arctic tundra. Arctic and Alpine Research 19:366-372.

*Chapin, F. S., III. 1983. Direct and indirect effects of temperature on arctic plants. Polar Biology 2:47-52.

*Chapin, F. S., III. 1984. The impact of increased air temperature on tundra plant communities, pp. 143-148. In: J. H. McBeath (ed.), The Potential Effects of Carbon Dioxide-induced Climatic Changes in Alaska. School of Agriculture and Land Resources Management. University of Alaska, Fairbanks.

*Chapin, F. S., III. 1987. Environmental controls over growth of tundra plants. Ecological Bulletins 38:69-76.

*Chapin, F. S., III. 1989. The cost of tundra plant structures: evaluation of concepts and currencies. Am. Nat. 133:1-19.

Chapin, F. S. III, R. Jefferies, J. Reynolds, G. Shaver and J. Svoboda (eds.), Physiological Ecology of Arctic Plants: Implications for Climate Change. Academic Press, New York.

Chapin, F. S., III, and G. R. Shaver. 1981. Changes in soil properties and vegetation following disturbance of Alaskan arctic tundra. Journal of Applied Ecology 18: 605-617.

Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to manipulation of light, temperature, and nutrients in a field experiment. Ecology 66: 564-576.

Chapin, F. S., III, and G. R. Shaver. 1985. The physiological ecology of arctic plants, pp. 16-40. In: B. Chabot and H. A. Mooney (eds.), Physiological Ecology of North American Plant Communities. Chapman and Hall, London. 351 pp.

Chapin, F. S., III, and G. R. Shaver. 1988. Differences in carbon and nutrient fractions among arctic growth forms. Oecologia 77:506-514.

Chapin, F. S., III, and G. R. Shaver. 1989. Differences in growth and nutrient use among arctic plant growth forms. Functional Ecology 3:73-80.

Chapin, F. S., III, and G. R. Shaver. 1989. Lack of latitudinal variations in graminoid storage reserves. Ecology 70:269-272.

Chapin, F. S., III, and G. R. Shaver. Experimental test of the sensitivity of tundra ecosystems to climate chnage. Science, submitted May 1991.

*Chapin, F. S., III, and P. R. Tryon. 1982. Phosphate absorption and root respiration of different plant growth forms from northern Alaska. Holarctic Ecology 5:164-171.

*Chapin, F. S., III, and W. C. Oechel. 1983. Photosynthesis, respiration and phosphate absorption by <u>Carex aquatilis</u> ecotypes along latitudinal and local environmental gradients. Ecology 64:743-751.

Chapin, F. S., III, G. R. Shaver and R. A. Kedrowski. 1986. Environmental controls over carbon, nitrogen, and phosphorus chemical fractions in <u>Eriophorum vaginatum</u> L. in Alaskan tussock tundra. Journal of Ecology 74: 167-196.

Chapin, F. S., III, J. B. McGraw and G. R. Shaver. 1989. Competition causes regular spacing of alder in Alaskan shrub tundra. Oecologia 79:412-416.

Chapin, F. S., III, N. Fetcher, K. Kielland, K. R. Everett and A. E. Linkins. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. Ecology 69:693-702.

Chapin, F. S., III, R. Jefferies, J. Reynolds, G. Shaver and J. Svoboda. 1991. Arctic plant physiological ecology: A challenge for the future. In: F. S. Chapin, III, R. Jefferies, J. Reynolds, G. Shaver and J. Svoboda (eds.), Physiological Ecology of Arctic Plants: Implications for Climate Change. Academic Press, New York. Accepted for publication.

Chapin, F. S., III, R. Jefferies, J. Reynolds, G. Shaver and J. Svoboda. 1991. Arctic physiological ecology in an ecosystem context. In: F. S. Chapin, III, R. Jefferies, J. Reynolds, G. Shaver and J. Svoboda (eds.), Physiological Ecology of Arctic Plants: Implications for Climate Change. Academic Press, New York. Accepted for publication.

Chester, A. L., and G. R. Shaver. 1982. Reproductive effort in cottongrass-tussock tundra. Holarctic Ecology 5: 200-206.

Chester, A. L., and G. R. Shaver. 1982. Seedling dynamics of some cottongrass tussock tundra species during the natural revegetation of small disturbed areas. Holarctic Ecology 5: 207-211.

*Evans, B. M., D. A. Walker, C. S. Benson, E. A. Nordstrand and G. W. Petersen. 1989. Spatial interrelationships between terrain, snow distribution and vegetation patterns at an arctic foothills site in Alaska. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):270-278.

*Everett, K. R., G. M. Marion and D. L. Evans. 1989. Seasonal geochemistry of an arctic tundra drainage basin. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):279-289.

*Fetcher, N. 1983. Optimal life-history characteristics and vegetative demography in <u>Eriophorum vaginatum</u>. J. Ecol. 71:561-570.

Fetcher, N., and G. R. Shaver. 1982. Growth and tillering patterns within tussocks of <u>Eriophorum vaginatum</u>. Holarctic Ecology 5: 180-186.

Fetcher, N., and G. R. Shaver. 1983. Life histories of tillers of <u>Eriophorum vaginatum</u> in relation to tundra disturbance. Journal of Ecology 71: 131-148.

Fetcher, N., and G. R. Shaver. 1990. Environmental sensitivity of ecotypes as a potential influence on primary productivity. American Naturalist 136:126-131.

*Gartner, B. L. 1982. Controls over regeneration of tundra graminoids in a natural and man-disturbed site in arctic Alaska. M.S. thesis, University of Alaska, Fairbanks.

*Gartner, B. L. 1983. Germination characteristics of arctic plants, pp. 334-338. In: Proc. 4th International Conference on Permafrost. National Academy Press, Washington, DC. 1524 pp.

Gartner, B. L., F. S. Chapin, III and G. R. Shaver. 1983. Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. Journal of Applied Ecology 20: 965-980.

Gartner, B. L., F. S. Chapin, III and G. R. Shaver. 1986. Reproduction by seed in Eriophorum vaginatum in Alaskan tussock tundra. Journal of Ecology 74: 1-19.

Giblin, A. E., K. J. Nadelhoffer, G. R. Shaver, J. A. Laundre and A. J. McKerrow. 1991. Biogeochemical diversity along a riverside toposequence in Arctic Alaska. Ecological Monographs, in press.

*Grulke, N. E., G. H. Riechers, W. C. Oechel, U. Hjelm and C. Jaeger. Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. Oecologia. Submitted.

*Hastings, S. J., S. A. Luchessa, W. C. Oechel and J. D. Tenhunen. 1989. Standing biomass and production in water drainages of the foothills of the Philip Smith Mountains, Alaska. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):304-311.

*Hilbert, D. W., T. I. Prudhomme and W. C. Oechel. 1987. Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO_2 flux through nonlinear modeling. Oecologia 75:466-472.

*Kane, D. L., L. D. Hinzman, C. S. Benson and K. R. Everett. 1989. Hydrology of Imnavait Creek, an arctic watershed. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):262-269.

Kielland, K. 1989. Processes controlling nitrogen release and turnover in arctic tundra. Ph.D. dissertation, University of Alaska.

*Kummerow, J., and B. Ellis. 1984. Temperature effect on biomass production and root/shoot biomass ratios in two arctic sedges under controlled environmental conditions. Canadian Journal of Botany 62:2150-2153.

*Kummerow, J., J. M. Mills, B. A. Ellis, and A. Kummerow. 1988. Growth dynamics of ccotton grass (Eriophorum vaginatum L.). Canadian Journal of Botany 66:253-256.

*Kummerow, J., J. M. Mills, B. A. Ellis, S. J. Hastings, and A. Kummerow. 1987. Downslope fertilizer movement in arctic tussock tundra. Holarctic Ecology 10:312-319.

Lechowicz, M. J., and G. R. Shaver. 1982. A multivariate approach to the analysis of factorial fertilization experiments in Alaskan Arctic tundra. Ecology 63: 1029-1038.

*Marion, G. M. and K. R. Everett. 1989. The effect of nutrient and water additions on elemental mobility through small tundra watersheds. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):317-323.

*Marion, G. M., S. J. Hastings, S. F. Oberbauer and W. C. Oechel. 1989. Soil-plant element relationships in a tundra ecosystem. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):296-303.

Mark, A. F., N. Fetcher, G. R. Shaver and F. S. Chapin, III. 1985. Estimated ages of mature tussocks of cotton sedge, Eriophorum vaginatum, along a latitudinal gradient in central Alaska. Arctic and Alpine Research

17:1-5.

*Matthes-Sears, U., W. C. Matthes-Sears, S. J. Hastings and W. C. Oechel. 1988. The effects of topography and nutrient status on the biomass, vegetative characteristics and gas exchange of two deciduous shrubs on an arctic tundra slope. Arctic and Alpine Research 20:342-351.

McGraw, J. B., and G. R. Shaver. 1982. Seedling density and seedling survival in Alaskan cottongrass-tussock tundra. Holarctic Ecology 5: 212-217.

McKinley, V. 1981. Effect of hydrocarbons and pH on litter decomposition and primary production in an arctic lake. M.S. thesis, Department of Biological Sciences, University of Cincinnati. 109 p.

Meininger, C. A., and D. A. Nelson. Variation in the tardigrade fauna of a dust-impacted arctic tundra. Holarctic Ecology, in press.

Meininger, C. A., and P. Spatt. 1987. Variation in moss and tardigrade species assemblages in a dust-impacted arctic tundra. Arctic and Alpine Research 20(1):24-30.

Miller, P. C., P. M. Miller, M. Blake-Jacobson, F. S. Chapin III, K. R. Everett, D. W. Hilbert, J. Kummerow, A. E. Linkins, G. M. Marion, W. C. Oechel, S. W. Roberts and L. Stuart. 1984. Plant-Soil processes in Eriophorum vaginatum tussock tundra in Alaska: A systems approach. Ecological Monographs 54:361-405.

Miller, P. C., P. M. Miller, M. Blake-Jacobson, F. S. Chapin, III, K. R. Everett, D. W. Hilbert, J. Kummerow, A. E. Linkins, G. M. Marion, W. C. Oechel, S. W. Roberts and L. Stuart. 1984. Plant-soil processes in Eriophorum vaginatum tussock tundra in Alaska: a systems modeling approach. Ecol. Monogr. 54:361-405.

*Miller, P. C., R. Kendall and W. C. Oechel. 1983. Simulating carbon accumulation in northern ecosystems. Simulation 40:119-131.

*Murray, K. J., J. D. Tenhunen and J. Kummerow. 1989. Limitations on Sphagnum growth and net primary production in the foothills of the Philip Smith Mountains, Alaska. Oecologia 80:256-262.

Nadelhoffer, K. J. 1990. A microlysimeter for measuring N mineralization and microbial respiration in aerobic soil incubations. Soil Science Society of America Journal 54:411-415.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver and J. A. Laundre. 1991. Effects of temperature and organic matter quality on C, N, and P mineralization in soils from six arctic ecosystems. Ecology 72:242-253.

Nadelhoffer, K. J., A. E. Linkins, A. E. Giblin and G. R. Shaver. 1991. Microbial processes and plant nutrient availability in arctic soils. In: S. Chapin, R. Jefferies, G. Shaver, J. Reynolds and J. Svoboda (eds.), Physiological Ecology of Arctic Plants: Implications for Climate Change. Academic Press. In press.

*Oberbauer, S. F., and W. C. Oechel. 1989. Maximum CO_2-assimilation rates of vascular plants on an Alaskan arctic tundra slope. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):312-316.

*Oberbauer, S. F., S. J. Hastings, J. L. Beyers and W. C. Oechel. 1989. Comparative effects of downslope water and nutrient movement on plant nutrition, photosynthesis, and growth in Alaskan tundra. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):324-334.

*Oberbauer, S., W. C. Oechel and G. H. Riechers. 1986. Soil respiration of

Alaskan tundra at elevated atmospheric CO2 concentration. Plant and Soil 46:145-148.

*Oechel, W. C. 1989. Nutrient and water flux in a small arctic watershed: an overview. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):229-237.

*Oechel, W. C., and B. Strain. 1985. Response of native species and ecosystems. In: Direct Effects of Increasing Carbon Dioxide on Vegetation. Department of Energy DOE/ER-0238.

*Oechel, W. C., and G. H. Riechers. 1986. Impacts of increasing CO_2 on natural vegetation, particularly the tundra. Proc. of Climate-Vegetation Workshop, NASA/Goddard Space Flight Center, Greenbelt, Maryland, January 27-29, 1986. pp. 36-42.

Oswood, M. W., K. R. Everett and D. M. Schell. 1989. Some physical and chemical characteristics of an arctic beaded stream. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):290-295.

*Pitelka, F. A., and G. O. Batzli. 1990. Distribution, abundance and habitat use of lemmings on the north slope of Alaska. Biol. J. Linnaean Soc., in press.

*Prudhomme, T. I., W. C. Oechel, S. J. Hastings and W. T. Lawrence. 1982. Net ecosystem gas exchange at ambient and elevated carbon dioxide concentrations in Tussock Tundra at Toolik Lake, Alaska: An evaluation of methods and initial results. In: J. H. McBeath (ed.), The Potential Effects of Carbon Dioxide-induced Climatic Changes in Alaska. Proc. of a Conference, April 7-8, 1982, School of Agriculture and Land Management, University of Alaska. Misc. Publ. 83-1:155-162.

Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie and J. D. Aber. 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO_2, climate and N deposition. Tree Physiology. (In Press).

Rastetter, E.B., and G.R. Shaver. A model of multiple element limitation for acclimating vegetation. Ecology, submitted January 1991.

*Riechers, G. I., T. I. Prudhomme and W. C. Oechel. A system for in situ temperature and carbon dioxide control at the ecosystem level: system description and evaluation of performance. In manuscript.

*Roach, D. A. 1983. Buried seed and standing vegetation in two adjacent tundra habitats, northern Alaska. Oecologia 60:359-364.

Shaver, G. R. 1981. Mineral nutrition and leaf longevity in an evergreen shrub, _Ledum_ _palustre_ ssp. decumbens. Oecologia 49:362-365.

Shaver, G. R. 1983. Mineral nutrition and leaf longevity in _Lidum palustre_: The role of individual nutrients and the timing of leaf mortality. Oecologia 56:160-165.

Shaver, G. R. 1986. Woody stem production in Alaskan tundra shrubs. Ecology 67: 660-669.

Shaver, G. R. 1991. Integrated ecosystem research in northern Alaska, 1947-1990. In: J. Reynolds and J. Tenhunen (eds.), Landscape Function: Implications for Ecosystem Response to Disturbance. A Case Study in Arctic Tundra. Springer-Verlag, New York, submitted February 1991.

Shaver, G. R., and F. S. Chapin, III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61(3): 662-675.

Shaver, G. R., and F. S. Chapin, III. 1984. Limiting factors for plant growth in northern ecosystems, pp. 49-60. In: T. R. Moore (ed.), Future Directions for Research in Nouveau-Quebec. McGill Subarctic Research Paper No. 39, McGill University, Montreal.

Shaver, G. R., and F. S. Chapin, III. 1986. Effect of NPK fertilization on production and biomass of Alaskan tussock tundra. Arctic and Alpine Research 18: 261-268.

Shaver, G. R., and F. S. Chapin, III. 1991. Production:biomass relationships and element cycling in contrasting arctic vegetation types. Ecological Monographs 61:1-31.

Shaver, G. R., and J. C. Cutler. 1979. The vertical distribution of phytomass in cottongrass tussock tundra. Arctic and Alpine Research 11(3): 335-342.

Shaver, G. R., and J. Kummerow. 1991. Phenology, resource allocation, and growth of arctic vascular plants. In: F. S. Chapin, III, R. Jefferies, J. Reynolds, G. Shaver and J. Svoboda (eds.), Physiological Ecology of Arctic Plants: Implications for Climate Change. Academic Press, New York. Accepted for publication.

Shaver, G. R., and M. J. Lechowicz. 1985. A multivariate approach to plant mineral nutrition: Dose-response relationships and nutrient dominance in factorial experiments. Canadian Journal of Botany 63: 2138-2143.

Shaver, G. R., B. L. Gartner, F. S. Chapin, III and A. E. Linkins. 1983. Revegetation of Arctic disturbed sites by native tundra plants, pp. 1133-1138. In: Proceedings 4th International Conference on Permafrost. National Academy Press, Washington, D.C. 1524 pp.

Shaver, G. R., F. S. Chapin III and B. L. Gartner. 1986. Factors limiting growth and biomass accumulation in Eriophorum vaginatum L. in Alaskan tussock tundra. Journal of Ecology 74: 257-278.

Shaver, G. R., K. J. Nadelhoffer and A. E. Giblin. 1990. Biogeochemical diversity and element transport in a heterogeneous landscape, the North Slope of Alaska, pp. 105-126. In: M. G. Turner and R. H. Gardner (eds.), Quantitative Methods in Landscape Ecology. Springer-Verlag, New York.

Shaver, G. R., K. J. Nadelhoffer, and A. E. Giblin. 1990. Climatic change, nutrient cycling and primary production in the Arctic landscape, pp. 184-185. In: V. M. Kotalyakov and V. E. Sokolov (editors), Arctic Research: Advances and Prospects (Part 2). Proceedings of the Conference of Arctic and Nordic Countries on Coordination of Research in the Arctic, Leningrad, USSR. Nauka, Moscow. 446 pp.

Shaver, G. R., N. Fetcher, and F. S. Chapin, III. 1986. Growth and flowering in Eriophorum vaginatum: Annual and latitudinal variation. Ecology 67:1524-1525.

Shaver, G. R., W. D. Billings, F. S. Chapin, III, A. E. Giblin, K. J. Nadelhoffer, W. C. Oechel and E. B. Rastetter. Global change and the carbon balance of arctic ecosystems. Final draft, to be submitted in June 1991 to BioScience.

Shaver, G.R., and F.S. Chapin, III. Long-term responses to factorial NPK fertilizer treatment in Alaskan wet and moist tundras. Arctic and Alpine Research, submitted March 1991.

Spatt, P. D. 1978. Seasonal variation of growth conditions in a natural and dust impacted Sphagnum (Sphagnaceae) community in northern Alaska. M.S. thesis, University of Cincinnati.

Spatt, P. D., and M. C. Miller. 1981. Growth conditions and vitality of Sphagnum tundra community along the Alaska Pipeline Haul Road. Arctic 34:48-54.

*Tissue, D. 1984. Physiological and growth response of <u>Eriophorum vaginatum</u> to elevated CO_2 and temperature in the Alaskan tundra. M.Sc. thesis, San Diego State University. 104 pp.

*Tissue, D. L., and W. C. Oechel. 1987. Physiological response of <u>Eriophorum vaginatum</u> to field elevated CO_2 and temperature in the Alaskan tussock tundra. Ecology 68:401-410.

Valentine, D. 1991. Influence of topography on soil acidity and hydrogen ion budgets in an arctic landscape. Ph.D. dissertation, Duke University.

*Walker, D. A., E. Binnian, B. M. Evans, N. D. Lederer, E. Nordstrand and P. J. Webber. 1989. Terrain, vegetation and landscape evolution of the R4D research site, Brooks Range Foothills, Alaska. Proceedings of Symposium: Ecology of an Arctic Watershed: Landscape Processes and Linkages. University of Ohio in Columbus, August 1987. Holarctic Ecology 12(3):238-261.

APPENDIX IV: ARCTIC LTER PERSONNEL DIRECTORY

Updated April 1, 1991

Bauman, Carolyn ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
cbauman@lupine.mbl.edu
fax (508)457-1548
Habitat: lakes and streams
Organism: all
Core Area: trophic structure, data management
Specialty: algae
Site: ARC

Bowden, W. Breck ....Dept. of Forest Resources
University of New Hampshire
Durham, NH 03924
(603)862-1020
w_bowden@unhh.unh.edu
fax (603)862-2030
Habitat: forest, streams, wetlands, tundra
Organism: microbes
Core Area: nutrient fluxes
Specialty: nitrogen, hydrology
Site: HBR
Alt Site: ARC, LUQ

Deegan, Linda A. ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
ldeegan@lupine.mbl.edu
fax (508)457-1548
Habitat: river
Organism: fish
Core Area: trophic structure
Specialty: fish production
Site: ARC

Fry, Brian D. ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
bfry@lupine.mbl.edu
fax (508)457-1548
Habitat: lakes, estuaries, forests
Organism: all
Core Area: trophic structure, nutrient fluxes
Specialty: stable isotopes
Site: ARC

Giblin, Anne E. ....MBL-Ecosystems
Woods Hole, Mass. 02543

(508)548-3705
agiblin@lupine.mbl.edu
fax (508)457-1548
Habitat: lake
Organism: water
Core Area: nutrient fluxes
Specialty: biogeochemical processing
Site: ARC

Hershey, Anne E. ....Dept. of Biological Sciences
University of Minnesota Duluth
Duluth, Minnesota 55812
(218)726-8200
rb13101@umndul.bitnet
fax (218)726-6360
Habitat: lakes and streams
Organism: insects, snails, fish
Core Area: trophic structure
Specialty: biotic interactions
Site: ARC

Hobbie, John E. ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
(Omnet)j.hobbie.mbl
jhobbie@lupine.mbl.edu
fax (508)457-1548
Habitat: lakes, streams
Organism: microbes
Core Area: trophic structure
Specialty: microbial processing
Site: ARC

Kipphut, George W. ....Center for Great Lakes Studies
600 E. Greenfield Ave.
Milwaukee, Wisconsin 52304
(414)649-3003
kipphut@csd4.csd.uwm.edu
fax (414)649-3005
Habitat: lakes
Organism: water/sediments
Core Area: nutrient fluxes
Specialty: geochemistry
Site: ARC

Kling, George W. ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
geo@lupine.mbl.edu
fax (508)457-1548
Habitat: lakes, streams
Organism: all
Core Area: trophic structure, nutrient flux
Specialty: stable isotopes

Site: ARC

Laundre, Jim ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
jiml@lupine.mbl.edu
fax (508)457-1548
Habitat: tundra
Organism: plants
Core Area: nutrient fluxes
Specialty: plant ecology
Site: ARC

Linkins, Arthur E. ....Dept. of Biology
Clarkson University
Potsdam, New York 13676
(315)268-6544
Habitat: tundra
Organism: microbes
Core Area: organic matter
Specialty: soil enzymes, microbial processing
Site: HFR
Alt. Site: ARC

McDonald, Michael E. ......Dept. of Chemical Engineering
University of Minnesota Duluth
Duluth, Minnesota 55812
(218)726-6306
mmcdonal@va.d.umn.edu
fax (218)726-6360
Habitat: lakes
Organism: fish
Core Area: trophic structure
Specialty: lake trout, fisheries
Site: ARC

Miller, Michael C. ....Dept. of Biological Sciences
University of Cincnnati
Cincinnati, Ohio 45221-0006
(513)556-9758
mmiller@ucbeh.bitnet
fax (513)556-5299
Habitat: lakes and rivers
Organism: plants
Core Area: primary production
Specialty: nutrients, primary production
Site: ARC

Moller, Bernie ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
bmoller@lupine.mbl.edu
fax (508)457-1548
Habitat: lakes and streams

Organism: all
Core Area: trophic structure, data management
Specialty: algae, water chemistry
Site: ARC

Nadelhoffer, Knute J. .....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
knute@lupine.mbl.edu
fax (508)457-1548
Habitat: tundra
Organism: microbes
Core Area: organic matter
Specialty: nitrogen cycling, decomposition, plant chemistry
Site: ARC
Alt. Site: HFR

O'Brien, W. John ....Dept. of Systematics and Ecology
University of Kansas
Lawrence, Kansas 66044
(913)864-4375
wjob@ukanvm.bitnet
fax (913)864-5321
Habitat: lakes and streams
Organism: zooplankton, fish
Core Area: trophic structure
Specialty: zooplankton communities, predator foraging models
Site: ARC

Pallant, Julie ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
jpallant@lupine.mbl.edu
fax (508)457-1548
Habitat: office
Organism: microchip
Core Area: data management
Specialty: data management
Site: ARC

Peterson, Bruce J. ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
fax (508)457-1548
Habitat: streams, watersheds
Organism: all
Core Area: modeling/synthesis
Specialty: ecosystem analysis
Site: ARC

Rastetter, Ed ....MBL-Ecosystems
Woods Hole, Mass. 02543

(508)548-3705
erastett@lupine.mbl.edu
fax (508)457-1548
Habitat: tundra
Organism: all
Core Area: modeling/synthesis
Specialty: ecosystem modeling
Site: ARC

Schell, Donald M. ....Water Resources Center
Institute of Marine Sciences
University of Alaska Fairbanks
Fairbanks, Alaska 99775
(907)474-7115
d.schell(omnet)
fax (907)474-7204
Habitat: streams, watersheds
Organism: all
Core Area: primary production, trophic structure, organic matter, nutrient fluxes, modeling
Specialty: ecosystem analysis
Site: ARC

Shaver, Gaius R. ....MBL-Ecosystems
Woods Hole, Mass. 02543
(508)548-3705
gshaver@lupine.mbl.edu
fax (508)457-1548
Habitat: tundra
Organism: plants
Core Area: nutrient fluxes
Specialty: plant nutrition
Site: ARC

Witt, David ....Witt, David
IAB- Logistics
University of Alaska Fairbanks
Fairbanks, Alaska 99775-0180
(907)474-7641
fndlwl@alaska.bitnet
fax (907)474-6967
Habitat: tundra
Organism: humans
Core Area: site disturbance
Specialty: logistics, camp management
Site: ARC