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RECENT AND FOSSIL DIATOM ASSEMBLAGES FROM LAKES IN CENTRAL AND NORTHERN ALBERTA: ECOLOGICAL AND PALAEOECOLOGICAL INFERENCES

by

COLLEEN MARGARET PRATHER ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

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Abstract

Assemblages of diatom species (Bacillariophyceae) were analyzed from modern and fossil sediments taken from lakes located in central to northern Alberta. Ecological and palaeoecological inferences were made from the association of species in the samples. Diatom analysis from a long sediment core *ca.* 8200 years taken from Otasan Lake (northeast Alberta) indicated that warmer than modern climate influenced the lake by increasing diatom productivity between *ca.* 7300 to 5000 years BP. Peatland formation in the catchment then influenced the lake between *ca.* 5000 to 3100 years BP by lowering the pH, after which the acidity decreased slightly. Diatom analysis from a long sediment core taken from Mariana Lake (northeast Alberta) indicated that the response to a warmer than modern climate (between *ca.* 7500 to 5500 years BP) occurred in three stages. Initially the lake was unproductive, then water levels decreased and the lake became shallow. Finally, the lake was very turbid, eutrophic and had very high diatom populations between *ca.* 4300 to 2700 years BP, interpreted as a delayed response to the warmer climate.

The modern assemblages of diatom species in the surficial sediments of 93 lakes located in northern to central Alberta was examined. Water depth and concentrations of magnesium, bicarbonate and total phosphorus (TP) significantly influenced the distribution of diatom species. A model was developed to infer concentration of TP in lake water, based on sedimentary assemblages of diatom species. The correlation between observed and diatom-inferred TP concentration, using weighted-averaging unimodal statistics, was high and significant ($r^2=0.80$; $p\leq0.05$). This model was applied to the fossil sedimentary diatom record retrieved from seven lakes in Alberta. This

model can be used to infer lake water TP concentration between 4 to 87 μg TP/l. Most of the fossil assemblages were statistically ($p \leq 0.05$) similar to the modern assemblages. Inferences of TP concentration for those samples were accepted. Two common limitations of the model were poor correlation between benthic species and TP concentration of epilimnetic water and fossil species outside of the range of modern species (as relative percent abundance). The model can be used to estimate natural variations of TP concentration within lakes, and thus may be of used in lake management strategies.

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One person alone can never accomplish a project of this magnitude. It is due to the support and encouragement of a family that makes it possible. I dedicate this thesis to my husband, Cliff Prather, and son Tavish Prather, who have both supported and encouraged me, but who have also sacrificed to allow me to accomplish this goal. The support of all of my other family members does not go unnoticed and it is very much appreciated.

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Many people provided the samples used in this project. Cores taken from Otasan Lake (sediment cores) and the associated catchment (peat cores) were retrieved by Dr. P. Kuhry and Mr. H. Friebe. Radiocarbon dates of these cores were provided by the Alberta Environmental Centre, Vegreville and the Lawrence Livermore Laboratory, California (one AMS ^{14}C date from the lake core). A NSERC operating grant to Dr. D.H. Vitt provided funding for a portion of the Otasan Lake study. Dr. G.M. MacDonald (McMaster University) generously provided samples for diatom analyses and the results of radiocarbon dating from the Mariana Lake core. Mr. D. Trew at Alberta Environmental Protection supplied lake sediment samples and water chemistry data for 87 of the modern lakes used in this study. Various people from the Limnology Lab (University of Alberta) provided sediment samples and water chemistry data for another 6 lakes used in the 93 lake modern data set. Funds and personnel from Alberta Environmental Protection, and a Canadian Circumpolar Institute (CCI) grant to C.M. Prather allowed for additional sampling of lakes in 1993. Some of the figures produced in this thesis were made possible by resources and personnel from the Department of Biological Sciences digital lab (DITRL).

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Chapter I. Recent and Fossil Diatom Assemblages from Lakes in Central and Northern Alberta: Ecological and Palaeoecological Inferences.

I.A. Introduction

Diatoms, in the class Bacillariophyceae, are unicellular algae, with a combination of pigments that give them a typical golden-brown appearance. Diatoms were first identified in 1703 (Round *et al.*, 1990), but it was not until 1786 when the term "Diatomaceen" was coined by O.F. Müller (Werner, 1977). Diatoms were initially considered to be animals (due to their ability to move), but not until the work of Kützing in 1844 were they classified as algae (see Round *et al.*, 1990). The cell walls of diatoms are composed mainly of glass (SiO_2) (Dixit *et al.*, 1992). Each cell is composed of two halves with species specific markings (such as pores or lines) either etched on the surface of the wall, or engraved through the wall. These markings are used to identify diatoms, to as a minimum, the taxonomic level of species. The unique markings on the cell walls of the diatoms probably initially led researchers to study them (Werner, 1977).

Algae in general, and diatoms specifically, can be found in any environment in which there is sufficient moisture (Round, 1981). Communities of diatoms develop in water (lentic=still and lotic=moving), in soil, and in aerial habitats (Patrick, 1977). They are restricted primarily by the availability of silica, but also by the abundance of other nutrients. Seasonal cycles of planktonic diatoms are commonly controlled by silica availability (Wetzel, 1975). Once the nutrient is depleted, and the ratio of it to other nutrients (e.g., phosphorus) becomes low, other diatom species (Kilham *et al.*, 1996) or more likely other algae (e.g., green algae or cyanobacteria) (Zhang & Prepas, 1996) can out compete them.

Dixit *et al.* (1992) estimated that more than 5000 diatom species exist in watery habitats in North America including many habitats in lakes. They are found floating in the water column (known as phytoplankton), and associated with submersed sediments (epipelon), sand (epipsammon), rocks (epilithon), and plants (epiphyton). The latter four communities are part of the phytobenthos. Diatom species living within the plankton are non-motile, and must rely upon water currents and internal buoyancy mechanisms to stay afloat. In contrast benthic species form filaments to extend into the photic zone, form colonies with mucilaginous sheaths to blanket a substratum, or possess a raphe for movement along a substratum. Interestingly, there is a positive correlation between water flow in a stream and total standing crop of the attached diatom community (Lee, 1989). Water flow appears to stimulate growth.

Species within these freshwater habitats are also influenced by and are adapted to microhabitat variations. An example of these variations is concentration of ions and molecules around the cell. In moving water (e.g., streams), nutrients and wastes are continually replaced and removed, respectively, from the vicinity of epilithic algae. In contrast, nutrients and wastes are not replaced or removed as quickly from epilithic algae in still water (e.g., slow streams or lake margins). Species are either exclusive to the epilithon in these two different habitats, or they must adapt their physiological functions to the specific conditions. In comparison, planktonic species in lakes must alter their position in the water column in order to adjust to levels of light, nutrients and waste products (as well as to avoid predators).

Diatoms are ecologically diverse and many species posses narrow optima and tolerances for many environmental variables (Dixit *et al.*, 1992). Initial ecological information and ecological significance was determined by researchers of the late 1800's and early 1900's by intensive sampling of diverse habitats, followed by microscopic examination of the samples (Werner, 1977).

Every species has its own ecological niche, defined by physical, chemical, and biotic components (Ricklefs, 1979). Planktonic diatoms, for example, bloom in the spring when water temperatures are low, and silica concentrations are high (Lund 1949, 1950). As the silica is depleted, other algae which are not dependent upon silica (such as green algae), but which can use other available nutrients out-compete the diatom species. It has been determined that the decline in silica, and not the relative abundance of other factors (e.g., nutrients, light, and temperature) is the major cause of the yearly decrease in the diatom populations (Wetzel, 1975). Eventually, spring planktonic diatoms are completely replaced by other species. This has also been observed in communities of epipelic diatom species (Round, 1960; Hickman, 1976). Thus, a temporal context can be part of a species' ecological niche.

Modern ecological studies have attempted to quantify the relationship between diatoms and environmental variables. Calibration sets are a data set consisting of chemical and physical variables, plus surficial sediments (with diatom assemblages) from many lakes within one region. Often, these lakes are selected to follow a predefined gradient for a specific variable (such as pH, total phosphorus or salinity). Hustedt (1937-39) devised five pH groups based upon the fairly rigid occurrence of diatom species across specific regions of the gradient. Other such studies have been done that classify diatoms into groups based upon their distribution across gradients of salinity (e.g., Kolbe, 1927) and organic content of the sediment (e.g., Round, 1957a, 1957b, 1957c). Nygaard (1956) derived indices, using Hustedt's pH groups, to quantify the relationship between pH and diatoms. From these indices, Meriläinen (1967) derived linear regression equations to also infer pH from a sample. Both studies were criticized for not including pH indifferent species (the fifth Hustedt pH group of species). Accordingly, Renberg and Hellberg (1982) devised a regression equation that included all five pH groups. Additional studies, this time in North America, studied the relationship between diatoms and pH (e.g., Charles, 1985; Dixit, 1986). Linear regression methods were used to derive inference equations for pH from these calibration data sets. In these studies there was the underlying assumption of a linear response between diatoms and pH.

Shelford and others first observed a unimodal response of species to an environmental gradient (as reviewed by ter Braak & van Dam, 1989). This was later extended to describe the response between diatom species and environmental variables. An underlying assumption is that each species has a single optimum and a tolerance along each environmental gradient. Secondly, it is assumed that species will be most abundant at sites with environmental variables close to the species optimum. A good estimate of a species optimum would come from the environmental value (e.g., for pH) at all sites in which the species was present, weighted by the relative abundance of the species at those sites (ter Braak & van Dam, 1989).

By the early 1990's unimodal statistics were being used on diatom calibration sets. A unimodal relationship between species abundance and an environmental gradient was assumed. Equations have since been developed for pH (e.g., Birks *et al.*, 1990; Charles *et al.*, 1990; Cumming *et al.*, 1992), dissolved organic carbon (Pienitz & Smol, 1993), salinity (e.g., Fritz, 1990; Cumming & Smol, 1993; Wilson *et al.*, 1996), nutrients (e.g., Hall & Smol, 1992; Christie & Smol, 1993; Bennion, 1994; Reavie *et al.*, 1995), water depth (Yang & Duthie, 1995) and surface water temperature (Pienitz *et al.*, 1995). These equations are applied to the diatom assemblages from modern or fossil lake sediments to quantitatively estimate the variable (e.g., pH) at that point in space or time. These models can be used on short or long lake sediment cores to infer the recent or complete history of lake development. This can provide background information that may be useful in devising lake management strategies.

The study of the history of a lake is known as palaeolimnology. The history studied may be a few decades to many thousand years. Palaeolimnologists observe fossil assemblages to infer past lake condition. These inferences can be made because the modern relationship between species and some environmental variables are known. Diatoms preserve well in most sediments, and are by far the most numerous preserved algal remains in lake and ocean sediments (Round, 1981). Their remains in lacustrine sediments (siliceous microfossils) have long been used as a way to assess environmental changes over long periods of time. Diatoms are good bio-indicator fossils to use because they are produced in abundance, they preserve well in anoxic sediments, and they are sensitive to changing environment (Anderson *et al.*, 1986). Diatoms are used as a proxy for environmental change in a lake.

Some palaeolimnological studies have been descriptive (e.g., Pennington, 1943; Round, 1957a, 1964; Bradbury & Waddington, 1973; Hickman *et al.*, 1984). Interpretations in these studies were made using the known modern ecology of the dominant species to describe the condition of the lake. Changes in a lake were described as more or less eutrophic (e.g., Haworth, 1969; Hickman & Schweger, 1991a) or more or less acidic (Wolfe, 1994) in comparison to modern condition. Absolute values were not estimated for different periods. In comparison, some palaeolimnological studies have used derived statistical inference equations, and are quantitative. An equation derived to infer a variable (e.g., pH, dissolved organic carbon, salinity or total phosphorus) can be applied to fossil diatom assemblages in a sediment core to estimate the rate and magnitude of changes over time. Thus, estimates of lake water pH, based upon fossil assemblages, can be compared to modern measured pH.

Qualitative palaeolimnological studies can potentially describe the predominant conditions of the lake, for example water depth (average for a lake), algal community, productivity, salinity and pH. Conversely, quantitative studies can only describe one variable (e.g., pH), but in a statistically rigorous manner to allow for direct comparisons to modern condition. However, there are limitations to quantitative methods. First, it is assumed that the relationships between diatom species and environmental variables have not changed over time. Second, estimates of a variable are based on the fossil diatom assemblages found in samples. Only those fossil species found in the modern calibration set can be used to estimate the variable. Therefore, there needs to be high correlation between fossil and modern diatom assemblages. Third, some diatom valves (e.g. *Asterionella*) may be poorly preserved. Thus, a component of the community is not represented in the fossil assemblage. Fourth, dominant species in fossil assemblages may be rare or absent in the calibration set. Estimates for samples with these types of species may be poor. Finally, estimates for some fossil samples may be based on only a few species due to the poor correlation between fossil and modern assemblages.

In this study I analyzed recent and fossil diatom assemblages from lakes in Alberta. The first objective was to analyze post-glacial sediment cores from two lakes in northern Alberta. Long-term lake records from this area of the province are lacking and so this study will add to the information of post-glacial conditions in Alberta. The second objective was to gather a database of diatom distributions across Alberta lakes, and to determine the relationship of the assemblages to measured environmental parameters. From this database, a statistical model to infer a lake variable (to be determined after analysis of the results) would be derived. This could then be applied to diatom sedimentary records to quantitatively infer lake development in Alberta. Diatom calibration sets have been gathered for British Columbia, the Northwest Territories, Ontario, Michigan, Florida, England, Ireland, Norway, Sweden and other areas, but until now they have been lacking for Alberta.

In Chapter II the palaeolimnological record is examined for Otasan Lake, in northeastern Alberta. From the diatom species assemblages in the core, qualitative interpretations are made about development of the lake. There are a large number of lakes from this area, although only one other lake was studied with respect to a complete post-glacial sediment record (Vance, 1986). In that study, pollen and not diatoms were analyzed. There are many peatlands in this area of the province. It was hypothesized that the present acidity of the lake was caused by the development and expansion of the *Sphagnum* dominated peatlands in the catchment.

In Chapter III the post-glacial sediment core from Mariana Lake, located in northeast Alberta, but further south than Otasan Lake, is examined. At this site, the palynological record was analyzed (Hutton *et al.*, 1994), in addition to the record from the surrounding peatlands (Nicholson & Vitt, 1990). By analyzing the fossil diatom assemblages from the core, qualitative interpretations about the development of the lake are made. The first objective was to compare these three separate records. The second objective was to compare interpretations of development of this lake to interpretations of the development of lakes located north and south of it. The final objective was to examine the response of the lake to inferred Holocene aridity, as interpreted from the pollen record (Hutton *et al.*, 1994), and compare it to the response of other lakes to changing Holocene climate.

Diatom assemblages (from surficial sediments) and water chemistry (from epilimnetic water) from 93 lakes across central and northern Alberta are documented in Chapter IV. The first objective was to undertake an extensive examination of modern diatom assemblages from Alberta lakes. Diatom assemblages from the epipelon of lakes in central Alberta have been described with respect seasonal fluctuations (Hickman, 1976, 1978), space and time variations (Jenkerson & Hickman, 1983a), and heated water effects (Hickman, 1974). The effect of heated water on growth (Hickman & Klarer, 1974), photosynthetic efficiency (Hickman & Klarer, 1975), species composition (Hickman, 1982) and species variations over time and space (Jenkerson & Hickman, 1983b) on diatom assemblages from the epiphyton have also been described. Finally, Hickman (1979) described the phytoplankton succession from a lake in central Alberta. My study did not focus intensively on a few lakes, but rather on surficial sedimentary assemblages from many lakes. It is assumed that the surficial sediments contain a representation of algal communities in the lake over the previous few years (Dixit *et al.*, 1995). The second objective was to examine the relationship between diatom species assemblages and measured surface water chemistry. Data sets have been developed for other regions in North America (e.g., Agbeti & Dickman, 1989; Charles *et al.*, 1990; Christie & Smol, 1993; Cumming *et al.*, 1992; Pienitz & Smol, 1993; Wilson *et al.*, 1996; Whitmore, 1989) and Europe (e.g., Anderson *et al.*, 1993; Bennion, 1994; Birks *et al.*, 1990; Renberg & Hellberg, 1982), but they selected lakes to lie along a predefined environmental gradient (e.g., pH, salinity, or phosphorus). It is hypothesized that significant relationships between diatom species and environmental variables will be evident in a randomly generated data set.

From the large data set, deep and shallow lakes (wetlands in some cases) formed two distinct groups. In Chapter V, the deep lakes alone are analyzed for relationships between diatoms and environmental variables. It was hypothesized that significant relationships between diatoms and environmental variables would be evident in this mix of deep lakes from northern to central Alberta. From this, a statistical model for the most important variable in the data set is derived. It is also hypothesized that the relationship between diatom species and the water chemistry of Alberta lakes would be very different from the relationship between diatom species and lakes from other regions. This would be due to the variation in geology, climate, upland vegetation and soils between regions. The diatom inference model derived from this study is the first one based on a calibration set of Alberta lakes.

In Chapter VI, the model developed to infer total phosphorus concentration (Chapter V) is applied to the fossil diatom assemblages from eight post-glacial sedimentary records taken from seven Alberta lakes. Two of the cores were those described in Chapters II and III. The other six cores came from studies done by Hickman *et al.* (1984), Hickman (1987), Hickman and White (1989), and Hickman and Schweger (1991a, 1991b, 1993). There were four objectives of this study: to assess usefulness of this inference model, compare qualitative and quantitative palaeolimnological analyses, discuss limitations of inference models, and determine if some lake records should be disqualified from quantitative analyses.

Finally, this thesis concludes with a summation and general discussion in Chapter VII. The main points of the individual studies are restated along with some final thoughts.

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Chapter II. History of a presently slightly acidic lake in northeastern Alberta, Canada as determined through analysis of the diatom record.[1]

II.A. Introduction

Natural as well as human influences within a lake catchment can have subtle and obvious effects. Catchment vegetation influences lake characteristics, and hence components of the biota such as diatoms (Round, 1957, 1961, 1964; Haworth, 1969; Whitehead *et al.*, 1986; Ford, 1990). Decreased nutrient availability occurs through progressive leaching of nutrients from catchment soils (Quennerstedt, 1955). Nutrients are retained in the accumulating catchment biomass (Vitousek & Reiners, 1975; Bormann & Likens, 1979; Marks & Bormann, 1972) and lakes will become progressively more oligotrophic. Exhaustion of carbonates in the drainage area can lead to a decline in lake pH (e.g., McIntyre *et al.*, 1991). Palaeolimnological investigations conducted in Alberta and British Columbia have shown that effects of changes in catchment vegetation can be detected by analysis of diatom remains found in lacustrine sediment cores (e.g., Hickman & Schweger, 1991a; Hickman & Reasoner, 1994, 1998).

Northern Alberta is characterized by large areas of peatlands and associated lakes (Vitt, 1992; Halsey *et al.*, 1993). These peatlands influence the chemical characteristics of such lakes (Halsey *et al.*, 1997). The actual degree of alteration depends upon the type and extent of the peatland, size of the water body, regional climate and location of the peatland in the catchment (Jones *et al.*, 1986). In northeastern Alberta, catchments of acid sensitive lakes have more fen peatland compared to those of non-acid sensitive lakes (Halsey *et al.*, 1997). Generally, poor fens have more influence upon lakes than bogs due to greater flow-through even though both have pH values between 3.5 and 5.5 (Gorham *et al.*, 1984). Both are dominated by *Sphagnum* species (Halsey *et al.*, 1997).

Deglaciation began in northeastern Alberta *ca.* 11,000 years BP (Dyke & Prest, 1987). Spruce became dominant in open woodlands after the initial pioneering vegetation (MacDonald 1987a; Zoltai and Tarnocai, 1975; Vance, 1986). Today spruce (white and black) is an important component in some uplands and peatlands. Actual peatland

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[1] A version of this chapter has been accepted by Journal of Paleolimnology. Prather and Hickman.

development did not commence until *ca.* 6000 years BP in some sites north of latitude 54^0 (Zoltai and Vitt, 1990). Warm, dry conditions compared to the present day occurred until *ca.* 4000 to 3000 years BP in central Alberta (Hickman et *al.*, 1984; Hickman & Schweger, 1991a & b, 1993, 1996; Schweger & Hickman, 1989), and possibly only until *ca.* 6000 years BP in northern Alberta. However, no significant changes in upland vegetation have been evident in northern Alberta since before that time (Vance, 1986; MacDonald, 1987a). In contrast, there have been significant changes in regional peatlands in northern Alberta that provide evidence of a transition to a cooler, more moist modern climate between *ca.* 8000 to 4000 years BP (Zoltai & Tarnocai, 1975).

The purpose of this study was to examine the development of a small, presently slightly acidic lake in northeastern Alberta, whose catchment is dominated by *Sphagnum*, through analysis of the sedimentary diatom record. It is hypothesized that expansion of *Sphagnum* species in the catchment is responsible for present pH levels, because evidence exists that suggest other lakes of the region were initially alkaline, even saline (Vance, 1986).

Using the community climate model (CCM), climate in northern Alberta at *ca.* 9000 years BP was estimated to have been warmer, but not significantly drier than modern (Kutzbach, 1987). Between *ca.* 9000 and 6000 years BP temperatures were still warmer, and precipitation was lower than present. Higher temperatures and lower precipitation would result in aridity. The decline of birch in western Canada (from British Columbia to Alberta) between *ca.* 9000 and 6000 years BP corroborates increased aridity at this time (MacDonald, 1993). Even though there was little change in upland vegetation in northeast Alberta at that time, it is hypothesized that the diatom record may be more sensitive than the pollen record to climate changes. This is because diatoms have a shorter life-span, higher turnover rate and greater species diversity than upland vegetation species.

II.B. Site Description

Otasan Lake ($57^0\ 42'\ 26''$ N; $112^0\ 23'\ 15''$ W) is a small (3.44 km^2) kettle lake with a maximum depth of 7.5 m situated in the Birch Mountains of northeastern Alberta (Fig. II-1). Selected chemical and physical characteristics are presented in Table II-1. The present pH of the lake is slightly acidic (summer surface pH = 6.7). The Birch Mountains are an upland area to the west of the Athabasca River. They rise to a plateau about 700 m above sea level (a.s.l.), with peaks slightly higher than 750 m a.s.l.(Fig. II-1). This upland is the origin of many tributaries (Stringer, 1976) with water flowing to the Arctic Ocean via the Lake Athabasca and Athabasca River basins (Atlas of Alberta, 1984).

Bedrock geology of the area is Lower to Upper Cretaceous sandstone, shale, coal, bentonite and oil sands (Atlas of Alberta, 1984). Overlying the bedrock lies morainal and glaciolacustrine deposits (Turchenek & Lindsay, 1982). The common soils of the uplands are grey luvisols, drystic brunisols, and large areas of organic soils with permafrost (Turchenek & Lindsay, 1982).

Peatland cover in the Birch Mountain region varies from 0 % to greater than 85 % cover (Vitt, 1992), including fens, bogs and peat plateaus (Vitt 1992; Halsey *et al.*, 1993). Vegetation is Mixedwood Boreal Forest dominated by *Picea glauca, P. mariana, Abies balsamea, Pinus banksiana, Populus tremuloides, P. balsamifera, and Betula papyrifera* (Turchenek & Lindsay, 1982), with a ground cover of various shrubs and reindeer lichen (Atlas of Alberta, 1984). The surrounding lower region is classified as High Boreal (Strong & Leggat, 1992), while the Birch Mountain Uplands with high peat cover are classified as Boreal Subarctic (Vitt *et al.*, 1994).

The climate of the region is characterized by 80 or less frost-free days per year and 400-500 mm of total precipitation per year. Average temperatures range from -21^{0}C in January to 14^{0}C in July (Atlas of Alberta, 1984). The distribution of summer precipitation is similar throughout the region. Maximum summer temperature may be affected by topography (Longley & Janz, 1978).

A palynological study on nearby Eaglenest Lake by Vance (1986) showed that herbs colonized the area immediately after deglaciation. An open parkland with *Populus* and grasses succeeded these primary colonizers (Vance, 1986). Then, an open *Picea* and *Betula* forest became established, and by *ca.* 7500 years BP *Pinus* reached the area. Since then upland vegetation has been similar to present.

II.C. Methods

A 330 cm long sediment core was retrieved from Otasan Lake during the winter in 1992 using a Livingstone piston corer (Cushing & Wright, 1965) (Fig. II-1). The core was stored at *ca.* 4^0C until sampled. It was described before 1 cm^3 subsamples were taken from the centre of the core for diatom, chrysophyte stomatocyst and organic matter content analyses.

Three cores were also retrieved from the surrounding peatland during the summer using a McCauley peat corer (Fig. II-1) in order to determine when peat formation began through ^{14}C dating. Only basal dates, at the limnic sediment/peat interface, were determined for these three cores. The peat cores were not described.

Subsamples for diatom and total chrysophyte stomatocyst analyses were treated as described in Hickman *et al.* (1984). A minimum of 500 diatom valves was counted per slide. Identifications were determined using Krammer and Lange-Bertalot (1986, 1988, 1991 a & b), Hustedt (1930), Patrick and Reimer (1966, 1975), Germain (1981), and Cleve-Euler (1951). Total stomatocysts were enumerated simultaneously with the diatoms. Organic matter, determined as loss on ignition (LOI), was determined as described in Hickman *et al.* (1984).

Chronology was determined by radiocarbon dating a 10 cm segment of basal sediment (330-320 cm) and through an AMS date obtained from a spruce needle found at 140 cm. Linear interpolation was used to determine zonation dates.

Correspondence Analysis (CA) was used to describe the species variation and underlying environmental gradients in the fossil samples. Unimodal ordination analysis was used because the underlying gradient on the first axis was long (3.015 SD). CA is an ordination method that maximizes species dispersion along a hypothetical environmental gradient (ter Braak, 1987). This was performed using CANOCO (version 3.10) (ter Braak, 1988, 1990). All taxa with more than 1 % abundance in at least two samples were used. Diatom species used in the statistical analyses, and the corresponding numbers used on the biplot, are presented in Table II-2. Zonation of the diatom record was determined using stratigraphically constrained cluster analysis using a dissimilarity matrix of Euclidean distances. The computer program Tilia (version 1.11) was used to zone and graph the diatom stratigraphy.

There are many published inference transfer equations for pH (e.g., Charles, 1985; Flower, 1986; Dixit, 1986). These formulae were derived from study lakes located on the Canadian Shield (Dixit, 1986), the Adirondack Mountains (Charles, 1985), and at low elevations close to the sea (Flower, 1986). In this study, only formulae using Index B or multiple regression including alkalibiontic species were considered, because in zone 1 *Ellerbeckia arenaria* (Moore) Crawford, an alkalibiontic species, dominated and defined the assemblage. The formula of Dixit (1986) was used because it had the best estimation of modern pH at this site (Fig. II-8) and alkalibiontic taxa were considered as a separate group.

II.D. Results

II.D.1. Core Description and Chronology

The sediment core was homogeneous in colour ranging from 2.5 YR 1.7/1 to 10 YR 2/1 with no rapid transitions, laminations or clasts. A basal date of 8220 ± 110 ^{14}C years BP indicated that the record did not span the entire Holocene period. The spruce needle at 140 cm gave a date of 2930 ± 70 ^{14}C years BP. The boundaries of the four diatom zones, in years BP, were estimated from these two dates by linear interpolation.

II.D.2. Loss on Ignition (LOI) and Carbonates

There was little variation in the dry weight and organic matter composition of the sediment samples from the core (Fig. II-2). Dry bulk density was highest in zone 1, gradually decreased to the lowest values in zone 3, and then increased slightly again in zone 4. The organic matter content did not vary much over the core. Highest values were found in zone 1 and early in zone 2

II.D.3. Diatom and Chrysophyte Stomatocyst Stratigraphy

Cluster analysis was used to determine the zones with a cutoff point arbitrarily selected. Four zones were determined from this analysis (Fig. II-3 & II-4) and each is described below. Few diatom valves found in zones 1 and 2, but there was a large increase in zone 3 and stable numbers throughout zone 4 (Fig. II-3). Many of the valves from the lower samples were broken, while those in the upper samples were generally intact.

II.D.3.a. Zone 1: OL-1; 320 - 285 cm; > *ca.* 8200 - *ca.* 7300 ^{14}C years BP

This zone represents the early to mid Holocene. Diatom concentration was lowest during this zone (0.6 – 15 x 10^6/cc). The large benthic species *Ellerbeckia arenaria* (Moore) Crawford (20-46 %) dominated. Other components of this initial flora included the epipelic *Fragilaria construens* v. *venter* (Ehr.) Hustedt, and *F. pinnata* Ehr., along with the attaching species *Achnanthes lanceolata* (Bréb.) Grun., and *Cocconeis placentula* Ehr. Planktonic species were minor components (maximum representation 13%) (e.g. *Stephanodiscus niagarae* Ehr. and *Aulacoseira ambigua* (Grun.) Simonsen). All of these species were grouped as pH indifferent or alkaliphilic except for *Ellerbeckia arenaria* (Moore) Crawford. It was grouped as alkalibiontic.

II.D.3.b. Zone 2: OL-2; 285 - 195 cm; *ca.* 7300 - *ca.* 5000 ^{14}C years BP

This zone represents the mid-Holocene period. Initially, Fragilaria *construens* v. *venter* dominated. Then, planktonic species gradually increased in importance to account for 61% of the assemblage. As the planktonic population increased in importance the dominant planktonic species changed. Initially, the most numerous species was *Aulacoseira italica* (Ehr.) Simonsen followed by *Stephanodiscus hantzschia* Grun. , *A. ambigua* and then *S. niagarae.* Other important species included *Cyclotella stelligera* Cl. & Grun., *F. pinnata, F. brevistriata* Grun., *Achnanthes lanceolata* and *A. suchlandtii* Hustedt. In this zone, concentration of diatoms and stomatocysts at least doubled (11 – 157 x 10^6/cc and 11 – 58 x 10^6/cc, respectively) simultaneously.

II.D.3.c. Zone 3: OL-3; 195 - 145 cm; *ca.* 5000 - *ca.* 3100 ^{14}C years BP

This zone represents the latter half of the mid-Holocene to the first part of the late Holocene. Planktonic species continued to dominate, but there were still many benthic species with a total abundance never less than 35 %.

This zone was the most dynamic with rapid changes in dominant species at the beginning and at the end. Between the end of zone 2 and the beginning of zone 3 there was a rapid increase of *Tabellaria flocculosa* (Roth) Kütz. v. *flocculosa* Strain IIIp *sensu* Koppen (1975). It maintained a population representing more than 30 % of the entire diatom flora for the whole zone. This is an acidophilic taxon (Hustedt, 1957; Flower & Battarbee, 1985). Another acidic species of this zone was *Aulacoseira distans* (Ehr.) Simonsen. Other important species included the planktonic *Aulacoseira ambigua*, *A. italica*, and *Cyclotella stelligera* along with some benthic *Fragilaria* species.

Diatom concentration, compared to zone 2, doubled in this zone (70 – 307 x 10^6/cc) resulting in some of the highest values for the entire record. The number of stomatocysts fluctuated with a peak at 190 cm (62 x 10^6/cc), a rapid drop at 170 cm (16 x 10^6/cc), and the highest value at 160 cm (87 x 10^6/cc). The diatom to cyst ratio remained low (range: 3-13.5) and relatively constant in this zone except at 170 cm when an increase occurred corresponding to the stomatocyst population decline. Overall the diatom to cyst ratio increased from the previous two zones from an average of 0.33 (zone 1) to 1.5 (zone 2) to 6.2 (zone 3).

II.D.3.d. Zone 4: OL-4; 145 - 0 cm; *ca.* 3100 ^{14}C years BP to the present

This zone represents the latter half of the late-Holocene up to the present. At the beginning of this zone planktonic species decreased (to less than 15 %) while concomitantly the importance of benthic species increased. Benthic species dominated the whole zone representing more than 65 % of the entire assemblage.

The rapid decrease of *Tabellaria flocculosa* v. *flocculosa* Strain IIIp and the increase in small *Fragilaria construens* v. *venter*, which dominated for most of the remaining record, defined this zone. The other important species were *F. pinnata*, *F. brevistriata*, and varieties of *F. construens*. There were small occurrences of planktonic species beginning with *Aulacoseira ambigua* immediately followed by *Tabellaria* *flocculosa* v. *flocculosa* Strain IIIp, both with low but persistent populations to the modern sediments.

Diatom concentrations remained fairly constant over this whole zone (172 – 295 x 10^6/cc) with one peak at 20 cm (507 x 10^6/cc). The stomatocyst assemblage and diatom to cyst ratio were constant throughout this zone (9 – 27 x 10^6/cc, 6 – 25, respectively), but the diatom to cyst ratio was consistently highest in this zone (average = 16.4).

II.D.4. Statistics

Indirect ordination, Correspondence Analysis (CA), was used to analyze the species variation in the Otasan Lake core samples. CA axis 1 (λ_1= 0.465; 32%) and CA axis 2 (λ_2= 0.265; 18.2%) explained a total of 50.2 % of the diatom species variance (Fig. II-5). The zones derived from the core stratigraphy were included on the ordination diagram (Fig. II-5). This shows that the sample differentiation is sufficient to form distinct zones. Underlying environmental gradients were inferred from the species distribution on the CA plot (Fig. II-6). CA axis 1 was inferred to represent a gradient of pH, with increasing pH to the right. Acidophilic species such as *Tabellaria flocculosa* v. *flocculosa* Strain IIIp (157) (numbers after species names correspond to those given in Table II-2 and in Fig. II-6) and *Aulacoseira distans* (20) are found on the left, while alkaliphilic and alkalibiontic species such as *Cymbella sinuata* Greg. (167) and *Ellerbeckia arenaria* (165), respectively, are found on the right.

From the species scores, the underlying gradient on CA axis 2 was of nutrient level and/or lake depth. Both gradients increased towards the top of the diagram (Fig. II-5 & II-6). Benthic species are located at the bottom while planktonic and eutrophic indicator species are located at the top (Fig. II-6). Since the samples of zone 4 do not vary along either axis (except for the sample at 140 cm), they were inferred to be similar along both underlying gradients (Fig. II-5). Inferred gradients have not changed much since 130 cm.

The sample scores along the first two axes were plotted versus depth in the core to better interpret these underlying gradients (Fig. II-7). The zones established by the species assemblages were overlaid in this diagram. The scores along axis 1 began high, and positive and decreased into and through zone 2. Over zones 3 and 4 they were negative with the most negative scores in zone 3. This axis was inferred to represent pH with the highest pH values represented by high, positive scores and the lowest pH values represented by negative scores.

The inferred underlying gradient for CA axis 2 was nutrient level/water depth with inferred increasing values to the right. The scores on this axis increased up to the end of zone 2, decreased into zone 3 and at the beginning of zone 4 (Fig. II-7). The remainder of zone 4 was constant.

II.D.5. Inferred pH

Modern measured pH was 6.7, determined from one sample taken in July 1988 (Trew, 1991) and the estimated value using the formula of Dixit (1986) was 6.93. The inference formula derived by Dixit (1986) came from a remote set of lakes in south central Ontario. This formula, as compared to some others (e.g., Charles, 1985; Flower, 1986; Winkler, 1988), estimated the modern pH very well, and even though this study area and the one of Dixit (1986) were not identical, general trends in estimated pH were evident.

The inferred pH of zone 1 was alkaline, with the highest values of the whole record. All estimated values were more than 8 (Fig. II-8). The inferred pH decreased slowly over most of zone 2 as the community changed from benthic to planktonic (Fig. II-3 & 4). There was an inferred drop in pH between 250-240 cm to values less than 7.5, which corresponded to the absence of *Ellerbeckia arenaria*. The inferred gradient of pH along CA axis 1 suggested a larger change in pH over these two zones (Fig. II-7). The increase in pH at 200 cm corresponded to the peak of alkaliphilic *Stephanodiscus niagarae* and *Fragilaria construens* v. *venter* (Fig. II-4).

The lowest inferred pH values of the entire record occurred in zone 3 with an immediate drop at the beginning of this zone to less than 6.5. The large decrease at 190 cm corresponded to a rapid increase in importance of *Tabellaria flocculosa* v. *flocculosa* Strain IIIp. All inferred values were less than 6.5 (Fig. II-7 & II-8). The pH in zone 4 recovered slightly and then averaged at about 6.6. The recovery at 140 cm corresponded to the rapid decrease of acidophilic taxa.

Overall the sample scores along CA axis 1 also followed the reconstructed pH pattern with high reconstructed pH in zone 1, gradually decreasing values in zone 2, lowest values in zone 3, slight recovery and then stability in zone 4 (Fig. II-7 & II-8).

II.E. Discussion

II.E.1. Chronology

The 8200 year BP basal date indicates that the entire Holocene record was not retrieved. Nearby Eaglenest lake had a much longer sedimentary record, but more importantly its basal sediments were composed of sand and silty clay, and a late-glacial date of > 11,000 years BP was obtained (Vance, 1986). A longer sediment record was expected because deglaciation of the area had occurred by *ca.* 11,000 years BP (Dyke and Prest, 1987), and Eaglenest Lake and Mariana Lake had both longer sediment cores and older basal dates. Sometimes chunks of glacial ice, covered and insulated by drift, do not melt initially (Cole, 1979). A dry lake bed before *ca.* 8200 ^{14}C years BP was not suspected since early Holocene warmth was not as intense at this latitude as compared to more southern latitudes (Kutzbach, 1987). Other evidence indicates parkland vegetation, and hence drier conditions did not develop this far north (Hutton *et al.*, 1994). Finally, longer records have been identified from other northern sites (e.g., Hickman & White, 1989; MacDonald, 1987a, 1993; Hutton *et al.*, 1994).

II.E.2. Loss on Ignition

The consistent LOI values suggest a relatively stable catchment over the sediment record with no drastic changes causing an influx of organic matter to the sediments (Fig. II-2). The higher LOI in zone 1 may reflect a catchment that is unstable, and the drop in LOI in zone 2 may reflect a change in dominant catchment vegetation to a type that releases less organic matter (coniferous dominated vegetation). The low diatom productivity over zones 1 and 2 suggest that possibly the organic source is allochthonous rather than autochthonous or that algae other than diatoms were important.

II.E.3. Diatom and Chrysophyte Stomatocyst Stratigraphy and Palaeolimnological Interpretations

II.E.3.a. Zone 1: OL-1; 320 - 285 cm; >*ca.* 8200 - *ca.* 7300 ^{14}C years BP

The modern size of the peatland in the catchment and the overall distribution of peatlands across northern Alberta indicated the possible significance of natural acidification. Correspondence analysis of the diatom species data suggested underlying gradients of pH (on axis 1), and water depth and/or nutrients (on axis 2) (Fig. II-6). A high eigenvalue on axis 1 indicated good separation of the species data (ter Braak, 1987). Since no calibration functions for pH have been derived from this area, a previously published formula was used to infer past pH (Fig. II-8). There are three drawbacks to using this type of equation. First, there has to be correct identification of the species in various studies. Second, the pH inference is highly influenced by only a few species. Third, there is the assumption that the same association exists between the species and pH in different areas and at different times, and that the same pH preference group always applies. For example, in this study, zone 1 was defined by *Ellerbeckia arenaria* and zone 3 was defined by *Tabellaria flocculosa* v. *flocculosa* Strain IIIp. It is the presence or dominance of these two species that suggested changes, and give extreme estimates of pH. Even with these drawbacks the inference equations can still be used to show general trends.

The species composition of zone 1 represents an unusual assemblage due to the high proportion of *Ellerbeckia arenaria*, a species that has not been found in any modern samples from northern and central Alberta (Prather, personal observation). It is also present in very few other records (e.g., Rawlence, 1991; Hickman and Reasoner, 1994). This species is rarely observed but appears to be found presently only in boreal and montane lakes (Cleve-Euler, 1951) and is considered to be an appropriate indicator of large proglacial lakes and the late-glacial period (Round, 1957). Rawlence (1991) found this species preceding the development of the Younger Dryas in a lake in New Brunswick. Hickman & Reasoner (1994) recorded this species co-dominating the diatom record of an alpine lake in Yoho National Park, British Columbia during the Neoglacial with maximum development *ca.* 1600 years BP. Its appearance, subsequent dominance, as well as its decline coincided with increased, then decreased proportions of glacigenic sediments in the core. *Ellerbeckia arenaria* is a cosmopolitan benthic species. It can occasionally occur in fast-flowing mountain streams (Krammer & Lange-Bertalot, 1991a), and on rocks around the edges of lakes (Foged, 1974). It occurs in surficial sediments of a small, deep lake on the northern slope of Alaska (Foged, 1971). It has also been found in Lake Baikal (Zabelina *et al.*, 1951) and in post-glacial sediments from Iceland (Foged, 1974). It is widely distributed in northern North America and has a long circumpolar history. It is considered a species indicative of alkaline, oligotrophic and possibly clear waters (Evans, 1970), yet it co-dominated in the alpine lake in Yoho National Park when the lake would have been very turbid with glacigenic clays and silts (Hickman & Reasoner, 1994). *Ellerbeckia arenaria* then appears to be characteristic of unstable catchments and relatively high base conditions (Round, 1961; Hickman & Reasoner, 1994). Its presence in Otasan Lake does not imply the existence of a proglacial lake, even though a short-lived one was thought to have occurred in the area (Van Waas, 1974). This is because the basal date of this core was only *ca.* 8220 years BP, and deglaciation of this area is dated *ca.* 11,000 years BP (Dyke and Prest, 1987). The area in which Otasan Lake is located, and the surrounding lowlands, is classified as Boreal Subarctic and High Boreal, respectively. The uplands have slightly colder summer temperatures and less precipitation than the lowlands (Strong & Leggat, 1992). It is possible that the lake experienced a short growing season compared to present, as well as turbid water during this zone. This resulted in low diatom numbers and could also explain the low number of stomatocysts.

The high relative abundance of *Ellerbeckia arenaria* suggests high pH and shallow and nutrient poor water (Fig. II-7). Low nutrients may occur in the initial phase of a lake (Round, 1957, 1964; Wetzel, 1983). The pH model confirmed alkaline conditions at this time (Fig. II-8).

II.E.3.b. Zone 2: OL-2; 285 - 195 cm; *ca.* 7300 - *ca.* 5000 ^{14}C years BP

By *ca.* 7500 years BP, modern upland vegetation, dominated by *Pinus* and *Picea*, had become established (Vance, 1986) suggesting climatic conditions approximating modern since this time. However, this may be inaccurate as the few species that dominate the Boreal Forest may be climatically insensitive compared to the rarer or lower pollen producing taxa. Model simulations of Holocene climate changes suggest that between *ca.* 11,000 and 6000 years BP summer temperatures were warmer and winter temperature were cooler compared to the modern climate (Ritchie *et al.*, 1983; Kutzbach & Guetter, 1986). Sites in Alberta along ecotonal boundaries of the Boreal Forest also suggest higher summer temperatures along with less precipitation in the early to mid-Holocene (e.g., Hickman & Schweger, 1993, 1996). This was followed by a gradual shift to cooler and wetter conditions (Lichti-Federovich, 1970; White & Mathewes, 1986; Ritchie, 1983; 1984; Vance *et al.*, 1983). Also, peatland expansion in northern Alberta dates to more than 6000 years BP (Zoltai & Vitt, 1990), corresponding to the onset of cooler and wetter climate (Kuhry *et al.*, 1993). Thus, precipitation exceeded evaporation, and production exceeded decomposition enabling peatland expansion to occur.

Within this zone both diatom and stomatocyst numbers increased. Planktonic species gradually became more important until they dominated the flora with *Aulacoseira italica, A. ambigua,* and then *Stephanodiscus niagarae* (Fig. II-4) gradually replacing *Fragilaria construens* v. *venter. Stephanodiscus niagarae* is a species highly characteristic of large lakes (Bright, 1968) as well as mesotrophic to eutrophic conditions. *Stephanodiscus hantzschii* is also present in this zone. Its presence also suggests eutrophic conditions (Hustedt, 1949; Bradbury, 1975; Hickman, 1979). Other palaeoenvironmental records for Alberta (e.g., Hickman & Schweger, 1991a, 1991b, 1996; Schweger & Hickman, 1989; Hickman & Reasoner, 1998) suggest increased lake production during this part of the Holocene.

The gradual increase in dominance of the planktonic species may reflect rising water levels, and increased nutrient concentrations. Little alteration in dominant vegetation may imply a relatively stable climate, although short-term changes through perturbations and plant succession appear characteristic of the Boreal Forest (Delcourt *et al.*, 1983). It may also simply imply that the ecological thresholds of these species have not been exceeded. Little change in dominant boreal vegetation has been previously viewed as a lack of sensitivity to climate change (Beaudoin, 1993).

The successional changes in the planktonic diatoms suggest changes in the nutrient status of the water column. There was an increase along the inferred nutrient gradient over this zone (Fig. II-7). Dominant Boreal upland vegetation did not change over this time period, but peatlands were beginning to expand. Higher precipitation results in higher runoff, and removal of nutrients to downstream sources. Changes in the lake at this time were due to minor fluctuations in climate that resulted in higher nutrients in the water column for the planktonic diatoms.

Fires, which are a natural part of the Boreal Forest, are positively related to nutrient cycling. Increased fire activity is inferred in northwest Alberta between *ca.* 8500 and 6000 ^{14}C years BP (MacDonald, 1987b). Thus, another possible source of nutrients could have been from burning of the catchment.

Underlying gradients in the species data (Fig. II-6) suggest that high pH continued until the mid-Holocene (Fig. II-7). Estimated pH values indicated gradually increasing acidity (Fig. II-8). The drop in pH between 250 and 240 cm was because of the disappearance of *Ellerbeckia arenaria*, while the increase in pH at 200 cm was due to the peak of *Stephanodiscus niagarae*.

II.E.3.c. Zone 3: OL-3; 194-145 cm; *ca.* 5000 - *ca.* 3100 ^{14}C years BP

Planktonic species continued to dominate, but there were significant changes in the dominants in zone 3; diatom and stomatocyst numbers increased (Fig. II-3). The latter perhaps occurred in response to more transparent water. *Stephanodiscus niagarae* quickly disappeared from the record, and just as rapidly the acidophilic species *Tabellaria flocculosa* v. *flocculosa* Strain IIIp appeared and dominated. Other acidophilic species such as *Aulacoseira distans* and *Tabellaria flocculosa* v. *flocculosa* Strain IV also appeared. These striking changes in dominance by acidophilic species suggests a change from an alkaline to a slightly acidic lake. This change occurred over approximately 200 years beginning *ca.* 5000 years BP. The inferred pH is the lowest of the entire record within this zone (Fig. II-7 & II-8). All values were less than 6.5 (Fig. II-8). An immediate drop in pH occurred at the beginning of the zone corresponding to the rapid increase and dominance of *Tabellaria flocculosa* v. *flocculosa* Strain IIIp.

Peatlands are a prime source for the natural acidification of lakes through the release of hydrogen ions (Turner *et al.*, 1989; Halsey *et al.*, 1997), and organic acids (Wood, 1989), but not nutrients like upland vegetation (Bormann & Likens, 1979). As such, a decrease in nutrients would be expected with a natural acidification event. The underlying nutrient gradient along axis 2 decreased during this acidification event (Fig. II-7). Available nutrients were declining because of the catchment influence upon the lake. In addition, high percent organic soils in watersheds are also linked to acid sensitive lakes, while fens are more important than bogs in determining lake acidity in northeastern Alberta (Halsey *et al.*, 1997). The base of peat core 42B, the farthest from the modern lake margin, was dated at 8460 ± 150 ^{14}C years BP (Fig. II-1). The bases of the other two peat cores were progressively younger. This indicated peatland development towards the present day lake margin (P. Kuhry, unpublished data). Holocene climate at this time in northern regions was adequate for peatland development (e.g. Nicholson & Vitt, 1990; Zoltai & Vitt, 1990; Kuhry *et al.*, 1992, 1993; Hutton *et al.*, 1994). Peatland development in the Otasan catchment began *ca.* 8460 years BP. By *ca.* 5000 years BP it had reached sufficient size to have a major impact upon the lake.

II.E.3.d. Zone 4: OL-4; 145 - 0 cm; *ca.* 3100 ^{14}C years BP to the present

At the beginning of this zone there was a large decrease in planktonic species, specifically *Tabellaria flocculosa* v. *flocculosa* Strain IIIp. It is here that the condition of the lake is inferred to have undergone another major change over approximately 200 years beginning *ca.* 3100 years BP (145 cm).

Dominance by *Fragilaria construens* v. *venter*, and co-dominance by *F. pinnata, F. brevistriata* and *F. construens* v. *construens* suggests lower water levels, transparent water, and/or decreased nutrients in the water column that inhibited growth of planktonic species (Fig. II-7). The modern inlets of the lake all flow through peatlands of the watersheds before entering the lake (Fig. II-1). Decreases in water level could result from changes in flow pattern through the peatland, with sources blocked or altered by peat accumulation. It is more likely that water levels decreased rather than the lake water becoming more transparent because the lake is presently a "brown water" lake (true colour 66 Relative Units) and has a secchi depth of 1.5 m (Trew, 1991). This does not allow illumination of the sediments in most of the lake (Fig. II-1). Inferred pH changed little from beginning to end in this zone (Fig. II-8). Similar peatland vegetation over this entire zone are likely the reason. Since diatom concentrations were not much higher than in the previous zone, the diatom to cyst ratio reflects a decrease in stomatocyst productivity (Fig. II-3). Chrysophytes are predominantly planktonic (Sandgren, 1988; Smol, 1988) and a decrease in their numbers may also suggest a decrease in water level.

Inferred climate at Otasan Lake at the beginning of this zone is estimated to have been near modern. This was cooler than the early to mid Holocene (MacDonald, 1987b; Kuhry *et al.*, 1992, 1993). Modern conditions are estimated because the climate was already well established and modern in central Alberta by this time (Vance *et al.*, 1983). Peatland development was estimated to have begun more than 6000 years BP in northern Alberta (Zoltai and Vitt, 1990) and more than 7000 years BP in the Otasan Lake catchment based on the peat core basal dates. *Sphagnum* peat accumulation began earlier than *ca.* 7000 years BP at a Saskatchewan site, and dominated shortly after 1500 years at more northerly sites (Kuhry *et al.*, 1993). It has been speculated that development of ombrotrophic peatlands, and possibly permafrost, may have occurred within the Otasan Lake catchment (personal communication D.H. Vitt). Permafrost cycles were established by *ca.* 3700 years BP in northwest Alberta (Zoltai, 1993). The establishment of permafrost possibly caused the decline in lake water acidity *ca.* 3000 years BP. The onset of permafrost also corresponds to the beginning of the neo-glacial (cooler than mid-Holocene climate) (Halsey *et al.*, 1995). Climate that produce permafrost cycles resembles modern conditions (Zoltai, 1993). Thus, climatic conditions have been fairly similar since that time. This, along with the relatively static diatom record, suggests that modern conditions have existed since *ca.* 3100 years BP in the vicinity of Otasan Lake.

II.F. Conclusions

Major trends are summarized (Fig. II-9).

1. The sedimentary record spans at least 8200 years, but does not include the initial late-glacial stage of the lake. This record was analyzed to determine the development of

this presently slightly acidic lake. Changes in the lake have been linked to the development of the *Sphagnum*-dominated catchment.

2. Diatom concentrations have increased over the history of this lake. Increases occurred until *ca.* 5000 years BP suggesting improved conditions for diatom growth and/or preservation. Between *ca.* 5000 to *ca.* 3000 years BP an apparent increase in diatom concentration occurred. Since *ca.* 3000 years BP diatom concentrations have remained fairly constant.

3. The ratio of diatoms to chrysophyte stomatocysts was less than 7 until *ca.* 3100 years BP. The ratio increased and has remained at about 15 since *ca.* 2900 years BP perhaps reflecting higher nutrient levels.

4. Upland vegetation from a nearby lake was established *ca.* 7200 years BP. This suggests that the dominant climate patterns (precipitation, temperature, evaporation) had been established by that time. Evidence from Otasan Lake suggests that small changes have occurred in the climate since then, and that these changes affected the lake biota and wetland vegetation in the catchment.

5. The lake record began *ca.* 8200 years BP with a benthic and alkaline diatom assemblage dominated by *Ellerbeckia arenaria* (Moore) Crawford. At *ca.* 7300 years BP planktonic species began to increase and dominate indicating increased water levels, decreased turbidity, and increased nutrient levels. *Tabellaria flocculosa* (Roth) Kütz. v. *flocculosa* Strain IIIp *sensu* Koppen dominated the record from *ca.* 5000 to *ca.* 3100 years BP. The lowest lake water pH was inferred for this zone. From *ca.* 3100 years BP to the present *Fragilaria* species, primarily *F. construens* v. *venter* (Ehr.) Hustedt, dominated the diatom assemblage. Diatom productivity and inferred pH were interpreted as stable.

6. Catchment vegetation has influenced Otasan Lake over most of the Holocene. The diatom record suggests that the lake began shallow, turbid and very alkaline. By *ca.* 7000 to 6000 years BP mesotrophic to eutrophic diatom species dominated the lake. Nutrient supply was from fires and runoff through the soils of established forests. Peatlands were developing in the catchment. They significantly impacted the lake by *ca.* 5000 years BP because acidophilic species began to dominate by then. After *ca.* 3000

years BP acidophilic species declined, and cosmopolitan benthic species dominated. Thus, only insignificant changes in the catchment vegetation, and the lake have occurred since *ca.* 3000 years BP. Modern climate has existed in the Otasan Lake region since that time.

7. Inferred pH suggests that the lake was initially alkaline (> 8). The change from alkaline to slightly acidic conditions took place between *ca.* 8200 and *ca.* 5000 years BP. The pH gradually decreased over time to the lowest levels in the mid-Holocene with some recovery by *ca.* 3100 years BP. The decline of lake water pH is inferred to have been caused by the peatland-dominated catchment, which gradually increased in size since *ca.* 8460 years BP. The recovery in lake water pH is thought to have occurred from a change in the catchment such as blockage or alteration of inflow sources.

8. The diatom stratigraphy, CA analysis and reconstructed pH all indicate that lake quality has been relatively constant from *ca.* 3100 years BP to the present (Fig. II-4, II-7 & II-8).

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Table II-1. Some chemical and physical characteristics of Otasan Lake, Alberta. Recorded by Trew (1991) from a 1988 surface summer sample.

Variable (Units)	Value at 0 m
Dissolved Oxygen (mg/l)	9.4
Temperature (°C)	17.3
Conductivity (µs/cm)	26
Colour (Relative Units)	66
Secchi Depth (m)	1.5
pH	6.7
Total Alkalinity (mg/L $CaCO_3$)	9
Total Dissolved Solids (mg/l)	2.28
Total Phosphorus (µg/l)	27.9
Sodium (mg/l)	1.01
Calcium (mg/l)	2
Magnesium (mg/l)	1
Bicarbonate (mg/l)	10.74
Chloride (mg/l)	0.99
Sulphate (mg/l)	5.04

Table II-2. Diatom species used in the statistical analysis and the corresponding numbers used on the biplot.

Number	Species Name
4	*Achnanthes lanceolata* (Bréb.) Grun.
5	*A. laterostrata* Hustedt
6	*A. linearis* (W. Smith) Grun.
8	*A. peragallii* Brun & Herib.
9	*A. suchlandtii* Hustedt
11	*A.* cf. *subatomoides* (Hustedt) Lange-Bertalot
13	*Amphora pediculus* (Kütz.) Grun.
19	*Aulacoseira ambigua* (Grun.) Simonsen
20	*A. distans* (Ehr) Simonsen
21	*A. granulata* (Ehr) Simonsen
22	*A. italica* (Ehr) Simonsen
24	*A. perglabra* (Øestrup) Haworth
27	*Cocconeis disculus* (Schumann) Cleve
29	*C. placentula* Ehr
34	*Cyclotella radiosa* (Grunow) Lemmerman
35	*C. stelligera* Cleve & Grun.
40	*Cymbella delicatula* Kützing
69	*Fragilaria brevistriata* Grunow
74	*F. construens* v. *construens* (Ehr) Grun.
76	*F. construens* v. *venter* (Ehr) Hustedt
80	*F. leptostauron* v. *leptostauron* (Ehr) Hustedt
81	*F. leptostauron* v. *martyii* (Héribaud) Lange-Bertalot
85	*F. pinnata* Ehr
88	*F. virescens* Ralfs
117	*Navicula leptostriata* Joergensen
119	*N. pseudoscutiformis* Hustedt
121	*N. pupula* Kütz.
125	*N. seminulum* Grun.
152	*Stephanodiscus niagarae* Ehr
153	*S. parvus* Stoermer & Håkansson
156	*Tabellaria flocculosa* (Roth) Kütz. v. *flocculosa* Strain IV sensu Koppen
157	*T. flocculosa* (Roth) Kütz. v. *flocculosa* Strain IIIp sensu Koppen
158	*Tetracyclus lacustris* Ralfs
159	*Navicula cf. detenta* Hustedt
160	*N. cf. mediocris* Krasske
162	*Navicula cf. submuralis* Hustedt
165	*Ellerbeckia arenaria* (Moore) Crawford

Table II-2 Continued.

166	*Achnanthes calcar* Cleve
167	*Cymbella sinuata* Gregory
168	*Fragilaria parasitica* (W. Smith) Grunow

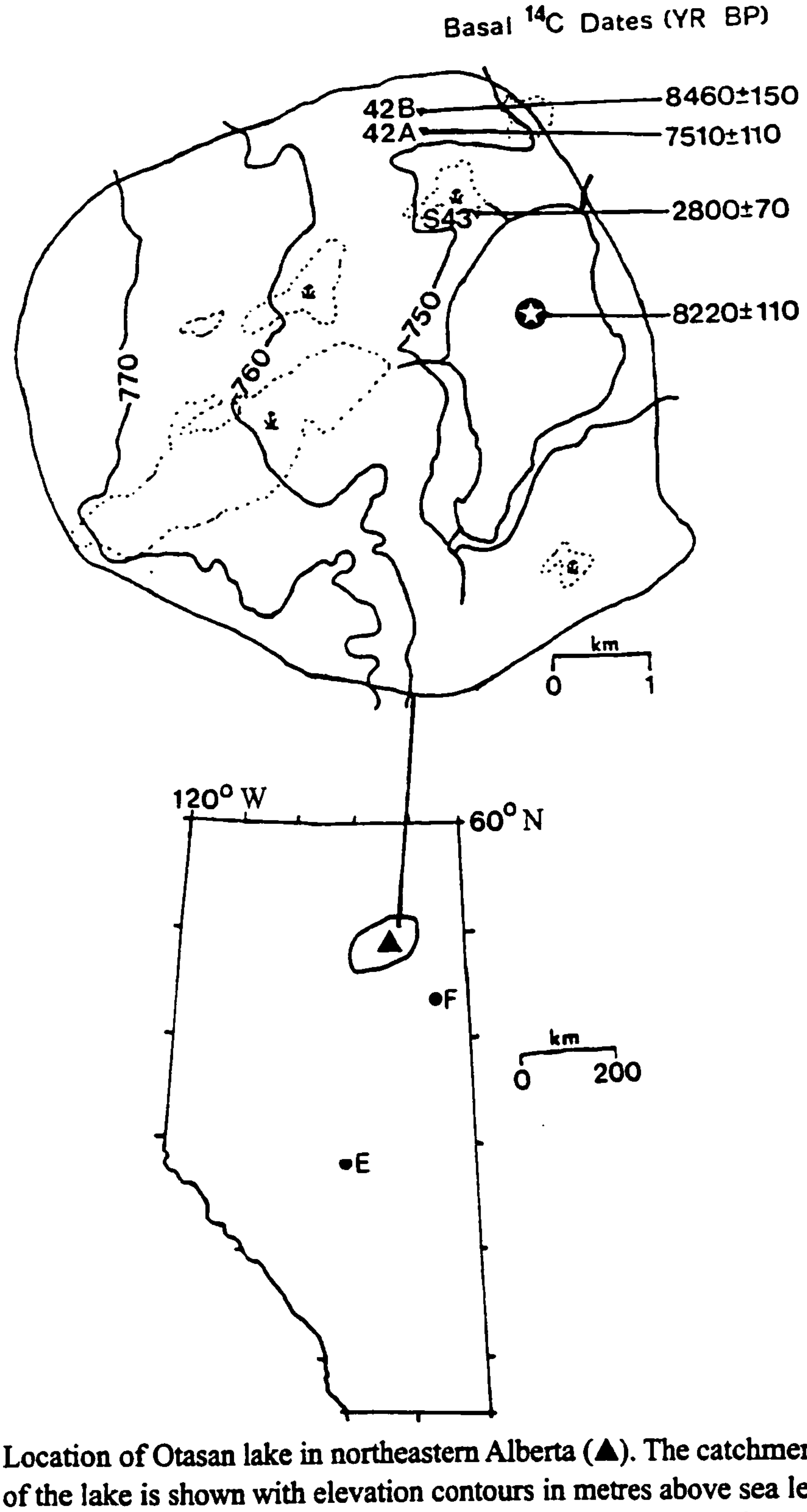

Figure II-1. Location of Otasan lake in northeastern Alberta (▲). The catchment basin of the lake is shown with elevation contours in metres above sea level. Core locations and basal dates of the sediment and peat cores are given. Locations of the cities of Edmonton (E) and Fort McMurray (F) are also shown.

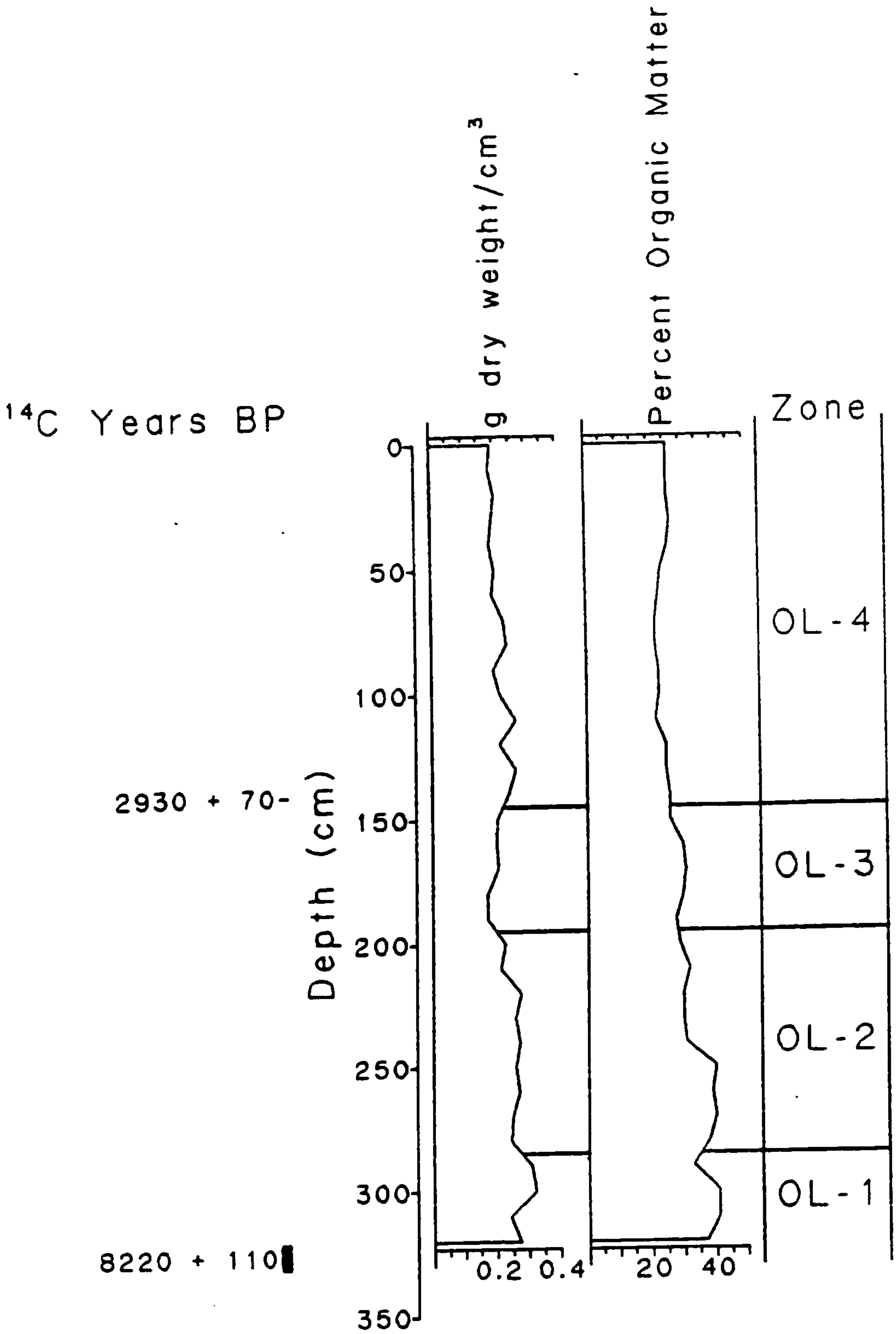

Figure II-2. Dry bulk density (gm dry weight/cm^3) and loss on ignition (% organic matter) values.

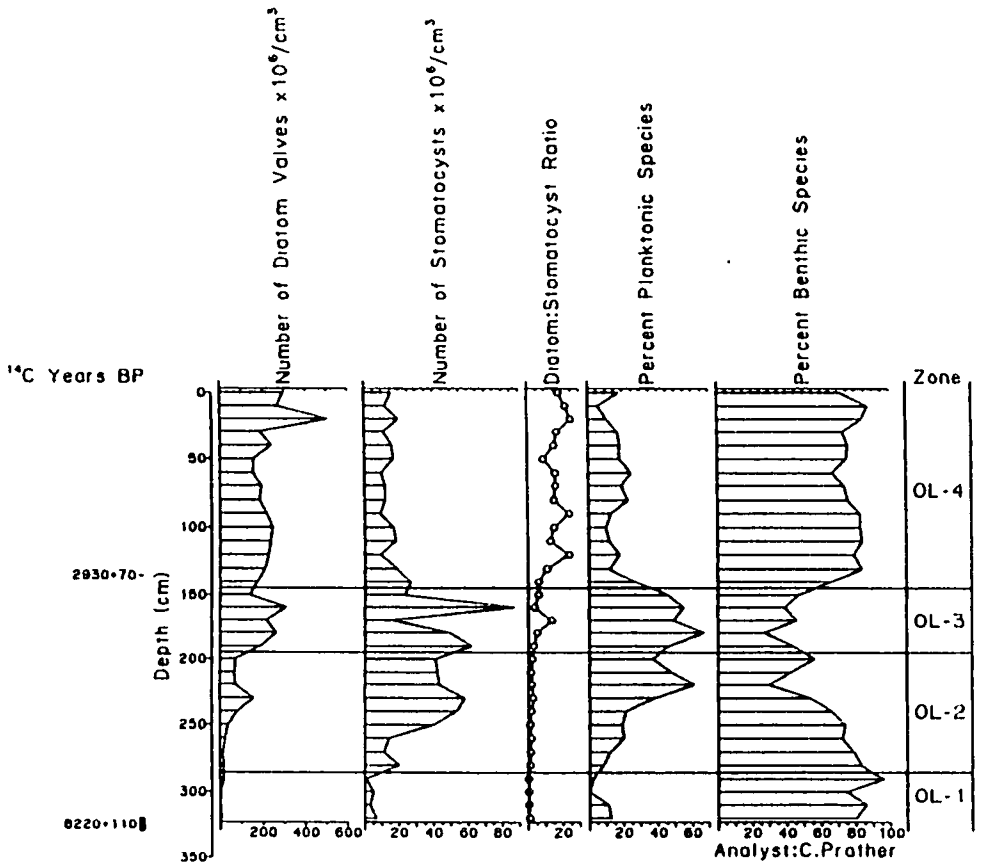

Figure II-3. Total diatom and stomatocyst numbers counted converted to number of individuals per cubic centimetre of sediment. The diatom to stomatocyst ratio was calculated from raw numbers counted in the sample. Percent planktonic and percent benthic species may not add up to 100 % because species with less than 1 % relative abundance in a sample were not included.

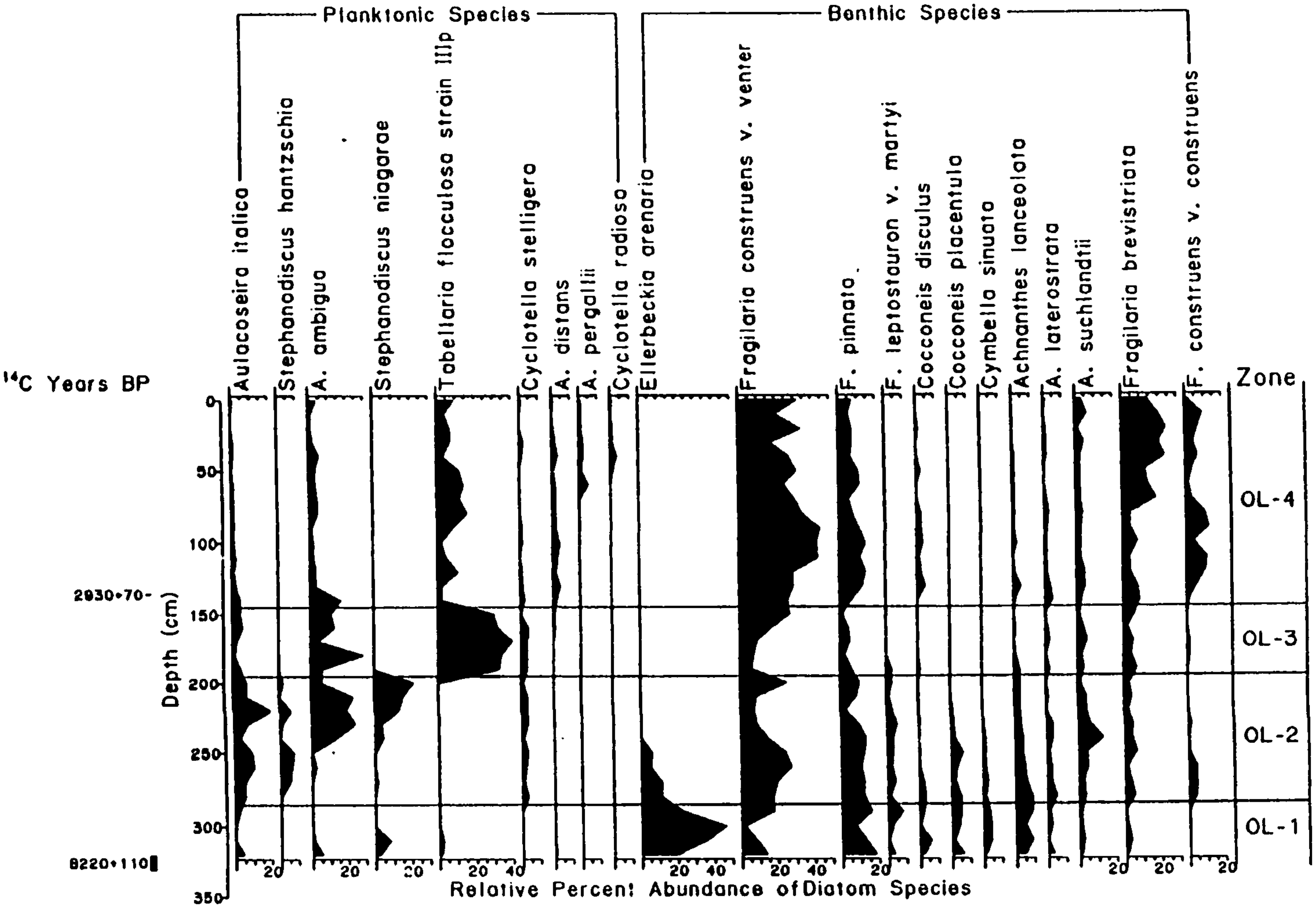

Figure II-4. Diatom stratigraphy for the Otasan Lake core. Only species with > 5% abundance in at least 5 samples were plotted. Species are represented as relative percent abundance. Zones were determined using cluster analysis.
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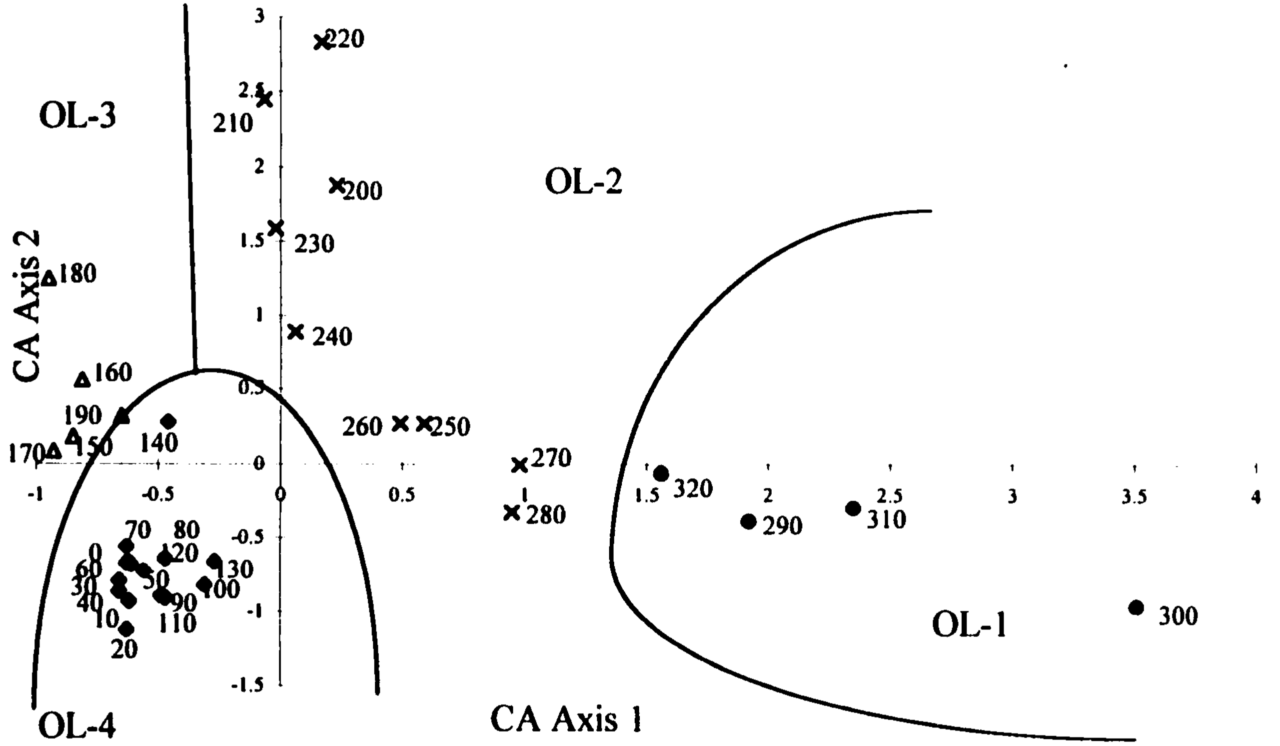

Figure II-5. Plot of the Correspondence Analysis (CA) scores of the first 2 ordination axes for the Otasan Lake core samples. The samples from the 4 zones of the diatom stratigraphy are indicated with different symbols [(ı) zone 1, (x) zone 2, (D) zone 3, (u) zone 4]. The diatom zones formed distinct groups of samples.

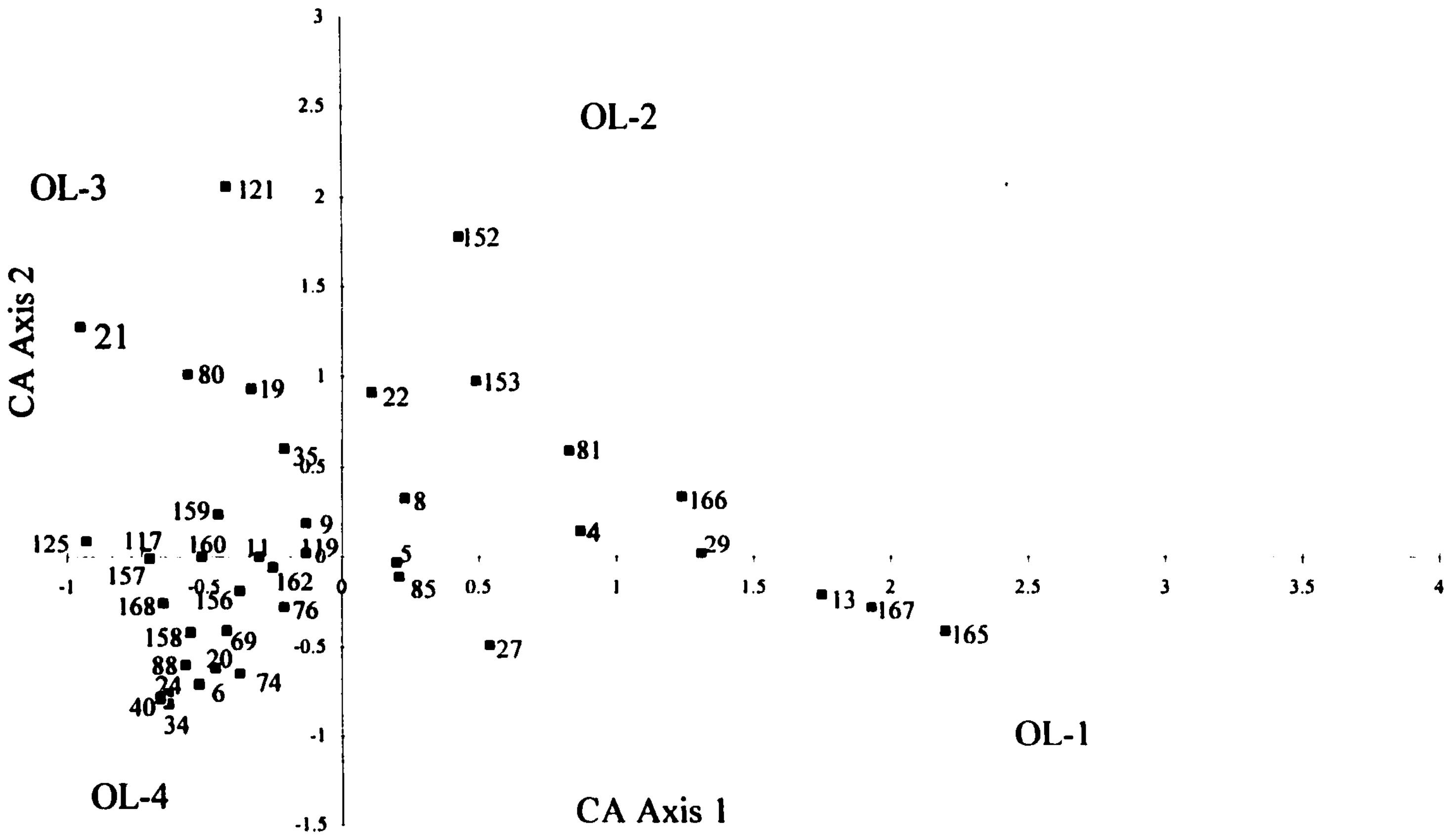

Figure II-6. Plot of the Correspondence Analysis (CA) scores of the first 2 ordination axes for the Otasan Lake core fossil species assemblage. Species with more than 1 % relative abundance in at least 2 samples were included. Corresponding species names are given in Table II-1.

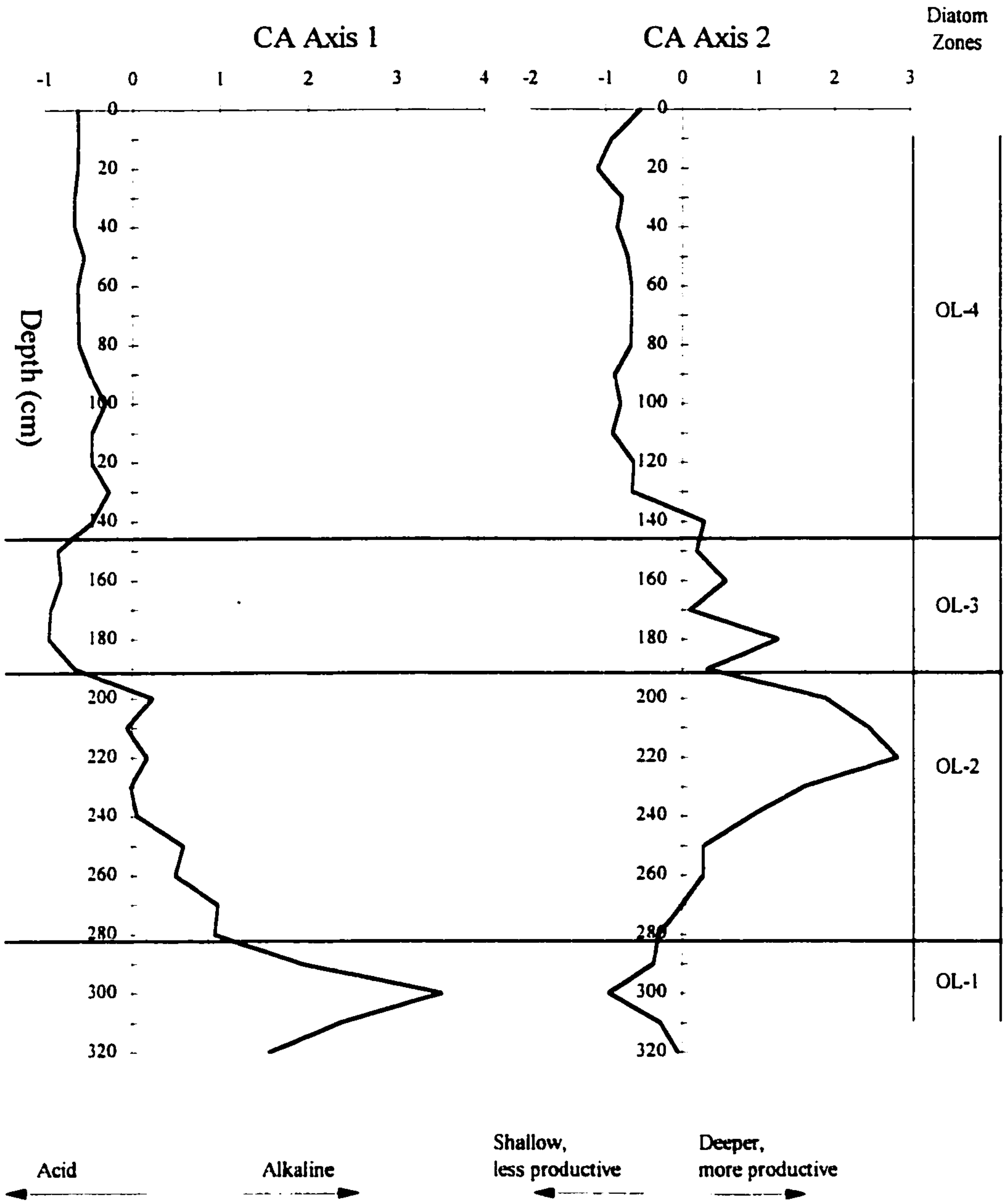

Figure II-7. The Correspondence Analysis (CA) scores from the first 2 ordination axes for the fossil samples plotted versus depth in the Otasan Lake core. The inferred underlying gradients on these axes are given.

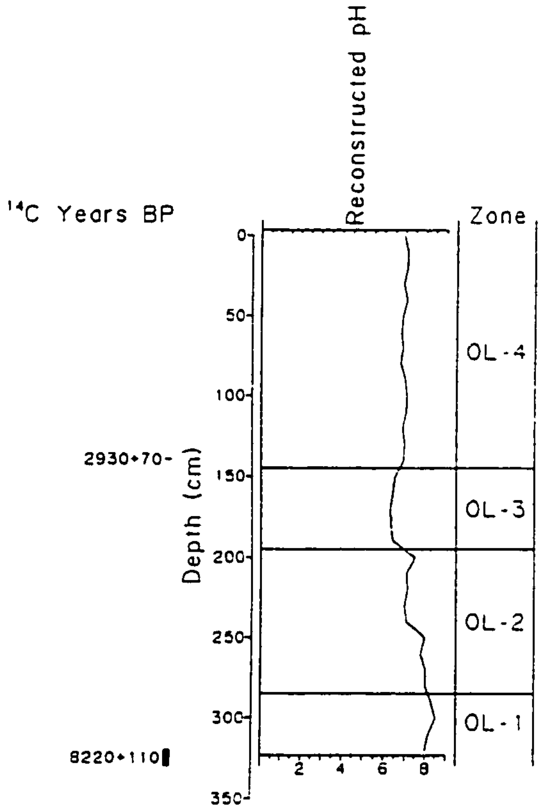

Figure II-8. Reconstructed pH for the Otasan Lake core using the derived Index B formula of Dixit (1986).

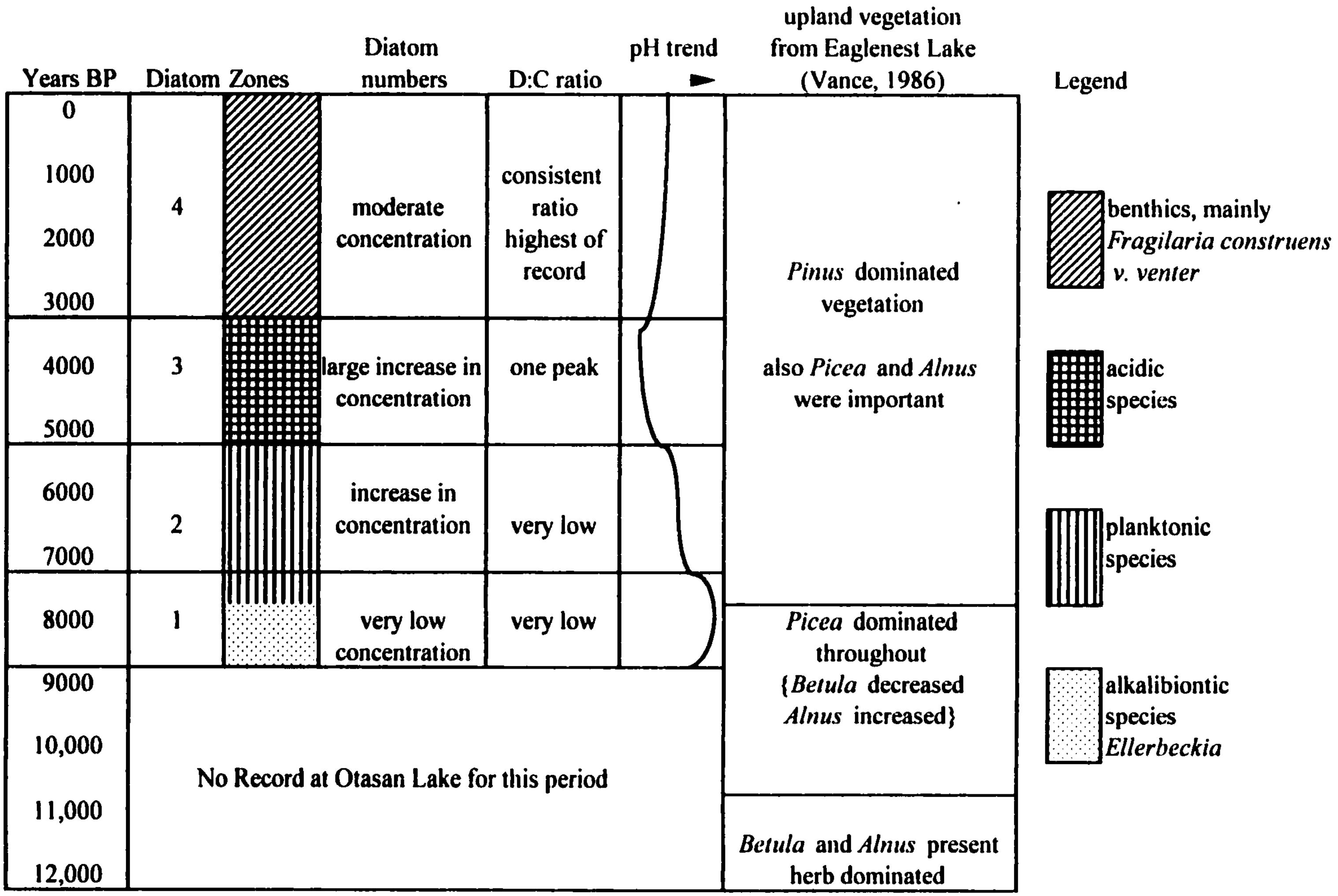

Figure II-9. Summary figure showing the major trends and inferences for the Otasan Lake record with the inferred upland vegetation record from Eaglenest Lake (Vance, 1986).

Chapter III. Effects of Catchment Development upon Mariana Lake, located within the Boreal Forest of Alberta, as interpreted from the Diatom record.[1]

III.A. Introduction

Lakes across northern Alberta remain largely unstudied with respect to their palaeolimnology. Accessibility is one of the contributing problems to their study. Yet with the advent of global warming, and with a general trend of increasing lake-water temperature in northern lakes (Schindler *et al.*, 1990) it is imperative that a detailed understanding of their history and evolution be developed. Most lakes in northern Alberta are small and not directly influenced by human activity.

Present day lake characteristics are the result of long term development that occurred in response to climate and catchment vegetation changes, as well as the underlying geology and internal lake processes. Within lake sediments, diatoms are often abundant and well preserved, so the actual history of a lake may be re-constructed by analyzing the remains of these siliceous algae. Diatoms are sensitive to chemical and physical factors and thus can be used to interpret lake development (e.g., Birks *et al.*, 1990; Hall & Smol, 1992; Yang & Duthie, 1995). Investigations of lake development and influencing factors have been conducted on several lakes lying along a west to east transect across the central region of Alberta, as well as on lakes in the Rocky Mountains of British Columbia and Alberta (Hickman & Klarer, 1981; Hickman *et al.*, 1984; Reasoner & Hickman, 1989; Schweger & Hickman, 1989; Hickman *et al.*, 1990; Hickman & Schweger, 1991a, 1991b, 1993, 1996; Hickman & Reasoner, 1994, 1998). Sometimes lakes and their biota respond more quickly to short term events than surrounding terrestrial communities (Hickman *et al.*, 1990). Often minor perturbations that do not significantly affect catchment vegetation do influence a lake. In these previous studies diatoms proved reliable in assessing water level fluctuations through changes in phytobenthic and phytoplanktonic assemblages as well as allowing increasing and decreasing salinity to be inferred through changing species composition. The diatom records were also sensitive markers of climate and catchment vegetation changes. Investigations elsewhere have also demonstrated the sensitivity of diatoms to

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[1] A version of this chapter has been submitted to Canadian Journal of Botany. Prather and Hickman.

environmental changes (e.g., Round, 1957a, 1957b, 1957c, 1957d, 1959; Round & Brooks, 1959; Haworth, 1969; Whitehead *et al.*, 1986; Wilson *et al.*, 1996; Chapter II).

The first objective was to examine the late Quaternary environment of Mariana Lake, Alberta. The lake was chosen because both the postglacial vegetation history (Hutton *et al.*, 1994) and peatland development (Nicholson & Vitt, 1990) in the catchment have been investigated in detail. This provided the second objective to compare the fossil pollen, peatland and diatom records. The third objective was to examine the effects of catchment vegetation changes and inferred increased aridity in the early to mid-Holocene upon the lake. The final objective was to compare the postglacial diatom and pollen records from other sites in Alberta to the one obtained from Mariana Lake. The effects of vegetation and inferred climate change on lakes from different areas across the province are considered in relation to development at Mariana Lake.

III.B. Site Description

Mariana Lake (55° 57′ N, 112° 01′W) is a small (16 ha), relatively shallow (6 m maximum depth) lake located on the Stoney Mountain Upland at an elevation of about 690 m (Fig. III-1). Bedrock comprises Cretaceous shale (Canadian Society of Petroleum Geologists, 1982) over which lies glacial till (Hackbarth & Nastasa, 1979) composed of gravel, sand and some clay (Ozoray & Lytviak, 1980).

The initial pioneering vegetation of the region was sparse and dominated by forbs and graminoids as determined by pollen analysis (Hutton *et al.*, 1994). By *ca.* 10,000 years BP, a *Picea glauca* forest replaced this vegetation. The major changes in dominant vegetation are summarized (Table III-1). Between *ca.* 10,500 to *ca.* 9000 years BP *Picea mariana/Sphagnum* peatlands began to develop (Hutton *et al.*, 1994), although Nicholson & Vitt (1990) concluded that the earliest peatland formation was due to hydroseral succession and lake-basin infilling *ca.* 8200 years BP. Earlier episodes of *Sphagnum* peatland development, not evident in the peat cores studied by Nicholson & Vitt (1990), may have occurred between *ca.* 10,000 to *ca.* 9000 years BP. It is possible that this peat decayed and was lost during the period 8000 to 6000 years BP (Hutton *et al.*, 1994) due to high decomposition.

After *ca.* 9000 years BP changes occurred that were likely caused by increased aridity. *Sphagnum*-dominated sites and *P. glauca* declined, while *Betula* increased. From *ca.* 7500 to *ca.* 5500 years BP *Populus* reached its maximum Holocene representation in the vegetation, although the expansion of Parkland into central Alberta during the mid-Holocene did not extend to the Mariana lake region. Throughout this arid period mesic sites remained, as indicated by the presence of *P. mariana*, *Abies* and *Larix*, while changes in *Typha* abundance suggested fluctuating water levels.

Sphagnum-dominated peatlands began to expand again *ca.* 6500 to 6000 years BP and paludification of mesic sites probably resulted in the decline of *Abies*. Initiation of extensive paludification occurred after *ca.* 5000 years BP. This was allogenically controlled and reflected a more, moist climate (Nicholson & Vitt, 1990). Paludification continued until *ca.* 2500 years BP when the present-day peatland complex was established.

Today the lake is situated within the Boreal Forest Ecoregion of northeastern Alberta (Strong & Leggat, 1981). Dominant arboreal vegetation includes *Picea glauca*, *P. mariana*, *Abies balsamea*, *Larix laricina*, *Pinus banksiana*, *Populus tremuloides* and *Betula papyrifera* (North, 1976; Strong & Leggat, 1981). Extensive, but discontinuous, peatlands occur in the area with fen being the dominant type (Nicholson & Vitt, 1990).

The regional climate is classified as boreal cold temperate (Walter, 1979). Mean annual temperatures at Fort McMurray (100 km north) and Calling Lake (100 km south) are 0.2 and 0.8 °C, respectively. Annual precipitation values are 464.7 and 462.7 mm, respectively (Atmospheric Environment Service, 1993). During July the mean daily temperatures at Fort McMurray and Calling Lake are 16.6 and 15.9 °C, respectively and total July precipitation values are 79.1 and 99.9 mm, respectively.

III.C. Methods

Dr. G.M. MacDonald (McMaster University) provided samples for diatom analysis. They were taken from the same core as fossil pollen samples analyzed by Hutton *et al.* (1994). Coring details, and sample storage can be found in Hutton *et al.* (1994). Bulk sediment from the core was radiocarbon dated and sedimentation rates calculated by fitting a second-degree polynomial to the dates (see Hutton *et al.*, 1994).

Samples for the diatom analysis ranged in size from 0.5 to 1.0 cm^3 with a sampling frequency of every 5 to 20 cm. These samples were prepared as described in Hickman *et al.* (1984). Known volumes of the diatom slurry were pipetted onto coverslips and allowed to air dry slowly. Visual examination of the diatoms showed them to be randomly distributed. Diatoms were mounted in Hyrax and at least 500 valves were enumerated. Identifications were made using Cleve-Euler (1951), Germain (1981), Hustedt (1930), Patrick and Reimer (1966, 1975) and Krammer and Lange-Bertalot (1986, 1988, 1991a, b). The total number of chrysophyte stomatocysts was determined, and chrysophyte scales were also enumerated and identified.

Diatom zones were determined using stratigraphically constrained cluster analysis using a dissimilarity matrix of Euclidean distances. The underlying variation in the species data was determined using indirect ordination, namely detrended correspondence analysis (DCA). Species are separated along hypothetical environmental gradients to maximize dispersion of the scores (ter Braak, 1987). The distribution of species and samples can be used to infer underlying environmental gradients in the fossil samples. Species with at least 1 % relative abundance were included in the DCA. Ordination results were determined with the computer programme CANOCO version 3.10 (ter Braak 1988, 1990).

III.D. Results and Discussion

III.D.1. Core Description and Chronology

The core, summarized from Hutton *et al.* (1994), measured 709 cm in length. The bottom 9 cm is a mottled calcareous clay, from 700 to 692 cm is laminated clay gyttja, 690 – 50 cm is a firm, dark brown gyttja, briefly becoming marly between 600 to 603, and 625 to 627 cm. The top 50 cm of sediment is unconsolidated and watery.

The radiocarbon dates are internally consistent and indicate continuous sedimentation from shortly after deglaciation to the present (Table III-2). The sediments contained some pre-Quaternary palynomorphs, and so it is possible that the basal date is too old. However, as pointed out by Hutton *et al.* (1994), the date of 11,300 ± 110 years BP agrees with the estimated time of deglaciation (Dyke & Prest, 1987). This is similar to other basal dates from northern (MacDonald, 1987a; Vance, 1986a) and central (Lichti-Federovich, 1970; Hickman & Schweger, 1991a, 1991b, 1993, 1996) Alberta.

To estimate the age of specific diatom zones and calculate sedimentation rates the second-degree polynomial of Hutton *et al.* (1994) ($Y = 4.87917 \times 10^{-6} X^2 - 0.119299X - 21.05713$), where X is the sample depth and Y is the corresponding age of the sample. The fit has an r-value of 0.98.

III.D.2. Diatom Stratigraphy Description and Interpretation

A total of 101 diatom species were encountered in the analysis, but only those with a relative abundance of ≥ 3% in at least 10 samples were included in the stratigraphic diagram. The diatom record does not cover the entire sedimentary record as no samples below 673 cm were available. Results are presented as relative percent abundance of the total count (Fig. III-2). Estimated rates of sedimentation (mm yr^{-1}) and diatom valve accumulation (number cm^{-2} yr^{-1}), along with total number of diatom valves, chrysophyte stomatocysts and scales cm^{-3} wet sediment is presented in Figure III-3. The diatom record for Mariana Lake spans *ca.* 9100 years BP. The diatom zones do not match with the pollen zones determined by Hutton *et al.* (1994).

III.D.2.a. Zone 1: D-ML-1; 673 – 600 cm; *ca.* 9100 to 7500 ^{14}C years BP

This zone begins in the early Holocene. No single diatom species dominated; instead several small planktonic and benthic species co-dominated. Planktonic dominants included *Cyclotella distinguenda* Hustedt, *C. pseudostelligera* Hustedt, and *Stephanodiscus parvus* Stoermer & Håkansson while benthic forms included *Fragilaria construens* v. *construens*, *Fragilaria brevistriata*, and *Fragilaria pinnata* (Fig. III-2). The two *Cyclotella* species were initially dominant, but by mid-zone *Stephanodiscus parvus* and *Fragilaria pinnata* Ehrenberg were important. Overall benthic species dominated but fluctuations in the importance of planktonic and benthic species and communities did occur.

Diatom numbers varied between 27 to 167 x 10^6 valves cm^{-3}, while valve accumulation rates were between 14 to 84 x 10^5 valves cm^{-2} yr^{-1} (Fig. III-3). Numbers of chrysophyte stomatocysts ranged between 9 to 60 x 10^6 cm^{-3} (Fig. III-3). A peak in the diatom to stomatocyst ratio occurred at the end of this zone. The ratio ranged from 1.4 to 10.4. Very few chrysophyte scales were found in this zone.

The beginning of this zone coincides with a change in the upland- vegetation from an open *Picea-Betula* forest to one dominated by *Betula* (Hutton *et al.*, 1994). *Sphagnum*-dominated sites and *P. glauca* also declined in this zone. However, increases in *Typha* pollen occurred. Such changes have been linked with increasing aridity (Hutton *et al.*, 1994). Fluctuations between benthic and planktonic communities suggests fluctuations in water levels, water clarity, nutrients or some biotic components, or a combination of the above. Biotic components may include herbivore populations or species assemblages, or possibly damming of the lake by beavers. Both the benthic and planktonic dominant species were small, in comparison to other diatom species (e.g., *Fragilaria construens v. construens* (Ehrenberg) Grunow, *F. brevistriata* Grunow, *F. pinnata*, *Cyclotella distinguenda*, *C. pseudostelligera* and *Stephanodiscus parvus*). Fluctuating water levels and turbulence favor small species. *Fragilaria* species are usually indicative of lower water levels (Hickman *et al.*, 1984; Hickman & Schweger, 1996). They are common epipelic taxa (Hickman, 1974) found in shallow alkaline lakes (Hickman *et al.*, 1984; Hickman & Reasoner, 1994, 1998) and the shallow littoral regions of deep lakes (Hickman & White, 1989; Hickman & Schweger, 1991a). They are also common pioneering forms in many lakes of glacial origin, and they dominated the early Holocene record in many Alberta lakes (Hickman & Schweger, 1991a, 1996). They occur abundantly over a wide nutrient range from oligotrophic to eutrophic lakes (Hall & Smol, 1992; Fritz *et al.*, 1993; Bennion, 1994; Reavie *et al.*, 1995). Their cosmopolitan nature makes interpretation of past events difficult. However, the record from Mariana Lake is different from other records in central Alberta and the Rocky Mountains because in Mariana Lake *Fragilaria* species co-dominated with species of *Cyclotella*. These small *Cyclotella* species are commonly found in mesotrophic to oligotrophic lakes (e.g., Agbeti & Dickman, 1989; Fritz *et al.*, 1993). *Stephanodiscus parvus* is also a small species, but estimates of optimum total phosphorus concentration (TP) indicate that it can tolerate oligotrophic to eutrophic water (11.4 to 200.9 μg TP l^{-1}) (e.g., Hall & Smol, 1992; Fritz *et al.*, 1993; Bennion 1994; Reavie *et al.*, 1995). The lakes used to derive these estimates varied in range of TP. Comparison of estimated optima of this species to all the other species in the respective calibration sets indicates that *S. parvus* can tolerate oligotrophic to mesotrophic, mesotrophic, or eutrophic water. The combination of all species in this section of the Mariana Lake core, suggest that the lake had an oligotrophic to mesotrophic status. In addition, interpretations from pollen, peatland, and diatom records suggest fluctuations in water levels during the early Holocene.

III.D.2.b. Zone2: D-ML-2; 600 – 535 cm; *ca.* 7500 to 6700 ^{14}C years BP

This zone corresponds to the early part of the mid-Holocene. Planktonic species dominated, representing more than 55% of the diatom assemblages in all samples. *Cyclotella distinguenda* and *C. pseudostelligera* were again important, but the long, delicate *Fragilaria nanana* and *F. tenera* also became important by mid-zone. Many of the valves of these latter two species were intact suggesting little sediment disturbance. Only small portions of the valves were broken and/or eroded. Among the few benthic species present were *Fragilaria construens* v. *construens*, *Achnanthes minutissima* Kützing, and *Cymbella microcephala* Grunow.

After the peak in diatom numbers at the end of zone 1, a rapid decrease occurred and thereafter numbers remained low until a peak at 545 cm. This peak coincided with an increase of *Cyclotella pseudostelligera.* Total number of diatom valves, and valve accumulation rates ranged between 28 to 280 x 10^6 valves cm^{-3} and 14 to 140 x 10^5 valves cm^{-2} yr^{-1}, respectively. In contrast, chrysophyte stomatocyst numbers were fairly consistent during this zone however, by the end of the zone they began to decrease. They ranged between 29 to 55 x 10^6 cm^{-3}. The ratio of valves to stomatocysts ranged between 0.59 to 5.1. It was in this zone that the largest number of chrysophyte scales was encountered. Two large peaks occurred at 585 and 545 cm, respectively. These scales were identified as those of *Mallomonas pseudocoronata* Prescott.

Total diatom numbers were lower than in zone 1. Poor preservation is not suspected since there were long, delicate valves in these sediments. Diatom numbers mirrored a large peak in *Cyclotella pseudostelligera* at 545 cm. By 540 cm there was still a large abundance of this species, but total diatom concentration had decreased dramatically. A change in nutrient concentration or sedimentation rate was inferred. The possibility exists that nutrients sufficient to enhance total diatom growth, but specifically *Cyclotella pseudostelligera* were present, then the sedimentation rate of other materials to the sediments increased which diluted the number of diatom valves in the sediment.

Assemblages dominated by planktonic species suggest constant water levels, while the excellent preservation of the long, delicate pennate species suggest little sediment disturbance, and calm, perhaps more transparent water. Planktonic species can more accurately reflect the chemistry of lake water as compared to benthic species due to their close association with the water column (Bennion, 1995). If this is correct then the planktonic diatoms of this zone indicate oligotrophic to mesotrophic conditions in the lake (Hall & Smol, 1992; Fritz *et al.*, 1993; Reavie *et al.*, 1995). Little has been reported about the ecology of *Cyclotella distinguenda*, except that it prefers water low in phosphorus (optimum 9.7 µg TP l^{-1}) (Fritz *et al.*, 1993).

The large number of *Mallomonas pseudocoronata* scales suggests alkaline water (Siver & Hamer, 1989). This species, plus a large number of stomatocysts and low diatom to cyst ratio suggest low nutrient concentrations. As a group, stomatocysts are considered mostly planktonic (Duff *et al.*, 1992; Duff & Zeeb, 1995). This, plus the dominance by planktonic diatom species suggests deeper water during this zone than in the previous zone.

The *Populus* pollen peak between *ca.* 7500 to 5500 years BP was inferred to be the results of a warmer than present climate, but not warm enough to allow development of parkland vegetation (Hutton *et al.*, 1994). This inferred warmer period was also evident at various locations further south in Alberta at Smallboy Lake (Vance *et al.*, 1983) and at Lofty Lake (Vance *et al.*, 1995). The locations of these lakes are indicated on Figure 1. At Moore Lake during this same interval, aridity was more intense as grassland and parkland vegetation replaced forest vegetation, saline planktonic diatom species dominated, and very low diatom numbers were found (Hickman & Schweger, 1996). Algal productivity was low due to Moore Lake becoming saline. A calibration equation (from pollen and climate data) applied to Lofty lake also suggested that the mid-Holocene was warmer and drier than at present (Vance, 1986b). North of Mariana Lake, at Eaglenest Lake, there was no evidence of increased aridity in the pollen record (Vance, 1986a). At Otasan Lake (also north of Mariana Lake), different from present conditions were inferred by the highest diatom numbers during this time, and by the dominance of eutrophic diatom species (Chapter II). At Mariana Lake, warmer than present climate affected the lake biota. Low diatom numbers likely resulted from low nutrient concentration in the water (as inferred by the dominant species), which was due to decreased water column mixing and re-suspension of nutrients from the sediments (as inferred from the preservation of delicate valves). The lower abundance of *Sphagnum* spores, and higher abundance of *Typha* and *Potamogeton* pollen (Hutton *et al.*, 1994), together with peatland development only via terrestrialization (Nicholson & Vitt, 1990) suggests a warmer climate. Based upon diatom and chrysophyte evidence, climate appears to have affected the lake in addition to the upland and wetlands in the catchment.

III.D.2.c. Zone 3: D-ML-3; 535 – 417 cm; *ca.* 6700 to 4300 ^{14}C years BP

A rapid change from planktonic to benthic species dominance marked the beginning of this zone. *Fragilaria construens* v. *venter* (Ehrenberg) Grunow replaced *Cyclotella pseudostelligera* as the dominant species (Fig. III-2). Benthic species accounted for 40 to 99% of the diatom assemblage. Planktonic species were important only occasionally, at 501 and 470 cm, corresponding to peaks of *Fragilaria nanana* and *Stephanodiscus parvus*, respectively.

Diatom accumulation rate ranged between 7 to 72 x 10^5 valves cm^{-2} yr^{-1}, while total valve number ranged between 13 to 144 x 10^6valves cm^{-3}. Two peaks in valve number were due to *Fragilaria construens* var. *venter*. Stomatocyst numbers fell in this zone, ranging between 4 to 44 x 10^6cm^{-3}. The diatom to stomatocyst ratio ranged between 0.91 to a maximum of 21 in this zone. Very few chrysophyte scales were found.

This zone represents the mid-Holocene when the *Picea-Betula-Populus* Forest was replaced by a *Picea-Pinus* forest *ca.* 5500 years BP (Hutton *et al.*, 1994). Dominant species did not change after this time. Extensive paludification by peatlands occurred after *ca.* 5000 years BP implying cooler and moister conditions compared to the early Holocene (Nicholson & Vitt, 1990). Peatland development over forested areas only occurs when precipitation exceeds evaporation (Gorham *et al.*, 1984). The change in dominant upland vegetation and the extent of peatland can influence water flow to, and nutrient concentrations in a lake (Chapter II). Peatlands around Mariana Lake have been poor fen since peatland initiation *ca.* 8000 years BP. Moreover, fewer nutrients are released when an area is covered with coniferous vegetation compared to deciduous vegetation (Hall & Smol, 1993). This results in reduced nutrient input into the lake.

The replacement of *Cyclotella pseudostelligera* by *Fragilaria construens* v. *venter* as the dominant species suggested that the lake was either shallower, or more transparent. Since epipelic species are influenced by variations in sediment chemistry (Round, 1957a, 1957b, 1957c, 1959), and many non-planktonic species are cosmopolitan with poor correlations to lake trophic status (Bennion, 1995) inferences about lake water nutrient status cannot be made at this time. A change in level of the lake water, or increased water clarity is likely due to the need for photosynthetically active radiation to reach the sediments to allow the benthic community to dominate. In addition, because of the overwhelming dominance by *Fragilaria construens* v. *venter*, changes in the upland vegetation (*ca.* 5500 years BP), and peatland (*ca.* 5000 years BP) had no effect upon the lake or at least the diatom community. In one study, changes in diatom assemblages were not always coincident with changes in the vegetation (e.g., Ford, 1990). There were single peaks by two planktonic species, namely *Fragilaria nanana* and *Stephanodiscus parvus* at 501 and 470 cm, respectively. These diatom peaks may have been short-lived responses to vegetation changes.

Farther north in Alberta, at Eaglenest Lake, modern vegetation had already been well established by this time (Vance, 1986a). Further south, forests were developing around Moore Lake, and the lake itself was becoming less saline (Hickman & Schweger, 1996). Evidence of cooling climate at this time was seen in the foothills region through boreal forest vegetation establishment around Fairfax Lake (Hickman & Schweger, 1991a), and in central Alberta through rising lake levels at Lake Wabamun (Hickman *et al.*, 1984), and general filling of lake basins (Schweger & Hickman, 1989). In southwest Saskatchewan, during this interval (*ca.* 6500 to 5200 years BP), the only occurrence of planktonic diatoms in a palaeolimnological record were interpreted as an indirect response to a warmer climate (Wilson *et al.*, 1997). Even though it may have still been warmer than present at this time (Vance *et al.*, 1995), the Holocene thermal optimum had passed, and conditions were approaching modern. From *ca.* 6700 to *ca.* 4300 years BP, benthic diatoms dominated, and lower lake levels were inferred. Modern vegetation began to develop after *ca.* 5000 years BP. Vegetation was inferred as modern *ca.* 2800 years BP, when *Abies balsamea* (prefers well drained sites) had declined to present abundance (Hutton *et al.*, 1994). It is suggested that the inferred warm climate from the previous zone had a longer lasting effect on the lake and possibly the upland through decreased lake and water table levels. Sandy outwash material is common in the Mariana Lake area (Nicholson, 1987). Water retention in sand is low due to large particle size (Ricklefs, 1979), thus high moisture levels are needed to raise or maintain a higher water level. It was inferred that well-drained sites became replaced because of the gradual decrease in *Abies balsamea* by *Picea* (Hutton *et al.*, 1994). Lake levels remained low (as indicated by diatom flora) and in some areas moisture laden soils were limited, because of adequate draining of sandy soils, until *ca.* 4300 years BP. Finally, changes were occurring in and around Mariana Lake, but the dominance by one cosmopolitan species makes interpretations of lake condition difficult if not impossible. So perhaps the diatom community was either unresponsive, or conditions within the lake were within the ecological thresholds of the dominant diatom species.

III.D.2.d. Zone 4: D-ML-4: 417 – 200 cm; *ca.* 4300 to 2700 ^{14}C years BP

The rapid decrease in *Fragilaria construens v. venter* and the concomitant rapid increase in *Aulacoseira ambigua* together with the near double increase in valve number defined the beginning of this zone. The persistent presence of *Aulacoseira ambigua* for *ca.* 1600 years characterized this zone. Fluctuations involving these two species did occur, but in general planktonic species (38 to 91% of population) were more important than those of the benthos. *Stephanodiscus parvus* was the only other planktonic species with a moderate abundance. Two prominent peaks occurred at 385 and 355 cm.

The patterns for number of valves (37 to 254 x 10^6 valves cm^{-3}) and diatom accumulation rate (52 to 356 x 10^5 valves cm^{-2} yr^{-1}) were nearly identical in this zone. The high number of valves at the beginning of this zone was due to the large population of *A. ambigua*. Three high peaks of total diatom valves occurred at 340, 295 and 210 cm. *A. ambigua* contributed predominantly to the first peak (75 % of all valves), while *F. construens v. venter* contributed predominantly to the latter 2 peaks (62 % and 52 % of all valves, respectively). The number of stomatocysts, 9 to 44 x 10^6 cm^{-3} in zone 4 was similar to the previous zone. The diatom to stomatocyst ratio was fairly constant (2.1 to 10.8). No chrysophyte scales were found in this zone. The inferred sedimentation rate (mm yr^{-1}) tripled from the previous three zones. The transition from a benthic to a planktonic-dominated assemblage suggested a major change in the lake.

This zone began in the first part of the late Holocene. Modern climatic conditions were established in central Alberta (Vance *et al.*, 1983; Hickman & Schweger, 1996) and in the Mariana Lake area (Hutton *et al.*, 1994) *ca.* 3000 years BP. *Pinus* and *Picea* dominated the landscape, while *Abies* gradually declined to present values *ca.* 2800 years BP. *Sphagnum* dominated peatlands were established by *ca.* 3000 to 2000 years BP (Nicholson & Vitt, 1990; Hutton *et al.*, 1994). At Eaglenest Lake there were no changes in dominant vegetation (Vance, 1986a), while peatland expansion resulted in the natural acidification of Otasan Lake (as interpreted by the dominance of acidophilic diatom species) (Chapter II). Moore Lake became fresh, with no further occurrences of saline diatom species (Hickman & Schweger, 1996). In central Alberta, Baptiste Lake became mesotrophic (Hickman *et al.*, 1990), while Fairfax Lake (Hickman & Schweger, 1991a) and Spring Lake (Hickman & White, 1989) declined in trophic status to oligotrophic conditions, with a flora dominated by benthic diatoms. Retention of nutrients in the catchment, decreased mixing of sediments and nutrients into the water column, and clearing of the water column (fewer suspended particles and plankton) allow a benthic community to proliferate.

Modern climate is cooler and moister than earlier in the Holocene (Kuhry *et al.*, 1993). Excess moisture results in higher water tables, fen development (Zoltai & Vitt, 1990), and runoff into lakes. Water can percolate through soils, pick up nutrients, and transport them to low lying lake basins.

The rate of sediment deposition tripled in this zone from the previous three zones, but diatom numbers were not diluted. This indicated that diatom and lake production were higher in this zone than in any other zone.

Modern ecological data suggests that *Aulacoseira ambigua* can tolerate variable levels of total phosphorus (TP) concentration. Estimated optimum TP ranges between 6.7 to 22.6 μg TP l^{-1} (Charles, 1985; Hall & Smol, 1992; Fritz *et al.*, 1993; Reavie *et al.*, 1995). These estimates came from separate calibration data sets with different ranges in TP, which may explain some of the variability in estimates. Overall, *A. ambigua* appears to be a mesotrophic species.

This species also prefers water high in dissolved silica (Kilham *et al.*, 1986). A shift in species dominance from *A. ambigua* to *Stephanodiscus parvus* in 2 Michigan lakes suggested increasing phosphorus availability, and a concomitant decrease in the silica to phosphorus ratio (Fritz *et al.*, 1993). In the early part of this zone *S. parvus* replaced *A. ambigua* as the dominant species in 2 samples. There may have been a slight change in the ratio of available nutrients in Mariana Lake, but probably not as definitively as in the Michigan lakes. Increased nutrient concentrations and/or increased water turbulence are hypothesized because of the appearance and dominance by *A. ambigua*. Since the growth of this species is enhanced by turbulent water (Lemmen *et al.*, 1988), it is inferred that between *ca.* 4300 to 2700 years BP the lake was well mixed.

The catchment, which was dominated by conifer forests, would not have been a rich source of nutrients for the lake (Hall & Smol, 1993). Thus, turbulent water, and re-suspension of sediment bound nutrients, were the likely cause of increased diatom numbers.

III.D.2.e. Zone 5: D-ML-5: 200 – 0 cm; *ca.* 2700 ^{14}C years BP to present

The rapid decrease and near elimination of *Aulacoseira ambigua*, combined with the drastic drop in total valve number and valve accumulation rates, defined the beginning of this zone. Although this species was present up to the modern sediment sample, its relative abundance was low compared to that of *Fragilaria construens v. venter*. Other species important in this zone were *Fragilaria pinnata, Achnanthes minutissima,* and *Navicula seminulum* Grunow. Benthic species accounted for between 58 to 90 % of the diatom assemblage. Planktonic species occurred sporadically, and in low number. The high relative abundance of benthic species, specifically *F. construens* v. *venter*, defined this zone.

Diatom number decreased rapidly at the beginning of the zone and thereafter remained low. Valves ranged between 10 to 61 x 10^6valves cm^{-3}, while accumulation rates ranged between 7 to 43 x 10^5 valves cm^{-2} yr^{-1}. In contrast, stomatocyst number was similar to those in zone 4, ranging between 9 to 27 x 10^6 cm^{-3}. The diatom to stomatocyst ratio decreased from zone 4, and ranged between 0.82 to 3.4. No chrysophyte scales were found in this zone. The inferred sedimentation rate decreased by one half of that in zone 4.

Modern vegetation patterns around Eaglenest, Baptiste, Wabamun, Smallboy and Fairfax Lakes was established by the time this zone began (Vance *et al.*, 1983; Hickman *et al.*, 1984; Schweger & Hickman, 1989; Hickman *et al.*, 1990; Hickman & Schweger, 1991a). Peatland development via paludification of the lower regions of the Mariana lake catchment (Nicholson & Vitt, 1990), and of other nearby catchments (Kubiw *et al.*, 1989) continued after *ca.* 3000 years BP. Conditions conducive to peat development over forested surfaces were present, and more of the catchment was stabilized by wetlands (Nicholson & Vitt, 1990). The rapid decline in *Aulacoseira ambigua* was inferred to be a response to lower nutrient concentrations, and perhaps less sediment disturbance and nutrient re-suspension through decreased water turbulence.

Little change has occurred in the lake over the last *ca.* 2700 years. This is a common feature among the development of Alberta lakes, although some lakes have also experienced more recent changes (i.e. the last *ca.* 1000 years BP). Otasan Lake (Chapter II) and Moore Lake (Hickman & Schweger, 1996) experienced no significant changes in the diatom records, and inferred lake quality after *ca.* 3000 years BP. Also, Wabamun Lake in central Alberta (Hickman *et al.*, 1984; Hickman & Schweger, 1991b), Fairfax Lake in the foothills region (Hickman & Schweger, 1991a), and Spring Lake in northwest Alberta (Hickman & White, 1989) experienced no significant changes since *ca.* 3000 years BP. Some exceptions to this include Baptiste Lake, which has become more eutrophic (Hickman *et al.*, 1990), and Cooking Lake which has become more shallower (Hickman, 1987), since ca. 1000 years BP. Relatively stable vegetation patterns that have existed in most of Alberta since ca. 3000 years BP (Hickman *et al.*, 1984; Hickman *et al.*, 1990; Hickman & Schweger, 1991a; Hutton *et al.*, 1994; MacDonald, 1987a, 1987b, 1989; MacDonald & Reid, 1989; Vance *et al.*, 1983; Vance, 1986a; White & Mathewes, 1986) are the likely reason why many palaeolimnological records have been unchanging since that time. Depending upon the catchment size, slope, vegetation patterns and lake biota, relatively constant conditions in the catchment may cause little, if any, alteration in the lake, and thus in the lake record. Small alterations in the catchment, such as fire or other disturbance, could impact the lake, and may be manifested in the lake record. This is one explanation as to why some records show constant assemblages since *ca.* 3000 years BP, and some do not. It is also possible that the diatom species in some lakes are tolerant to variation in quality of the lake water, while other species are not. Adaptable species would likely displace conservative species, and a record of succession would result.

III.D.3. Statistical Analysis

Variation in species assemblages between samples, and an investigation of the underlying environmental gradients in the samples from the core were determined using indirect ordination, namely Detrended Correspondence Analysis (DCA). The first two axes explained a total of 27 % of the cumulative variation (Fig. III-4 & III-5). The eigenvalue for axis 1 was high ($\lambda_1 = 0.609$). This indicated good separation of the species along the first axis. The value for axis 2 ($\lambda_2 = 0.337$) was lower than the value for axis 1, but it was still high enough to imply importance. The first two axes had long gradients (> 3 SD). The length of these axes indicated that the diatom species had unimodal distributions across the underlying gradients, and that samples at opposite ends had no species in common (ter Braak and Prentice 1988). Therefore, unimodal ordination methods were used to analyze the species data. Diatom species with ≥ 1 % relative abundance in at least three samples were included in the species DCA plot. There were 56 species that met this requirement. Species numbers are shown on the ordination biplot (Fig. III-5), while the corresponding names and authorities are given in Table III-3.

Samples had good separation along the two ordination axes (Fig. III-4). Included on the ordination diagrams are the zones that were determined in the diatom stratigraphy. Samples from zones 1 and 2 had similar scores along axis 1 (with similar variation), but they were separated along axis 2. Samples from these two zones were also separated from the majority of the samples in zone 4. Samples within zones 3 and 4 displayed variation along axes 1 and 2, while those within zone 5 varied only along axis 1. All zones showed good grouping of the fossil samples and many of the samples from zone 5 were close to those from zone 3 indicating similar species assemblages.

From the distribution of species along the ordination axes, underlying environmental gradients for those axes can be inferred and reconstruction of lake-history attempted. On the ordination diagram, species were positioned within the boundary of a zone in which they were most important (Fig. III-5). *Fragilaria pinnata* (Number 85) and *Cyclotella distinguenda* (Number 30), for example, were most important in zones 1 and 2, respectively (Fig. III-2). On the ordination biplot they were located within the boundaries of those two zones (Fig. III-5).

To determine underlying environmental gradients from the species distributions on the ordination diagram, their modern ecology must be known. Axis 1 was inferred to represent a gradient of nutrient status or trophic status that in turn may represent a gradient of production. *Aulacoseria ambigua*, *A. granulata* (Ehrenberg) Simonsen, and *Stephanodiscus hantzshii* Grunow (Numbers 19, 21, and 151, respectively) are eutrophic indicator species (Bradbury, 1975; Hickman, 1979; Hickman *et al.*, 1990). They were positioned on the left side of the diagram. *Cyclotella distinguenda* (Number 30) and *Anomoeoneis vitrea* (Number 16) are oligotrophic indicator species (Fritz *et al.*, 1993), and were positioned on the right side of the diagram (Fig. III-5). The gradient along axis 1 was then inferred to range from high nutrient status on the left to low nutrient status on the right.

The underlying gradient along axis 2 (unlike that along axis 1) separated zones 1 and 2, while zones 4 and 5 were not separated (Fig. III-4). The long fine, delicate species of *Fragilaria nanana* and *F. tenera* (Numbers 82 and 86, respectively), and the small robust *Stephanodiscus parvus* (Number 153) were positioned at the bottom and top, respectively, of axis 2 (Fig. III-5). Gradients of water turbulence and water depth were inferred. Samples representing lower water turbulence/higher water level were positioned at the bottom of the diagram. This was inferred from the excellent preservation of the delicate *Fragilaria* species that are often found as fragments (e.g., Hickman & Schweger, 1996). In samples with preserved and abundant *S. parvus*, positioned towards the top of the diagram, higher turbulence/lower water levels were inferred.

The DCA site scores for axes 1 and 2 were plotted against sediment depth in the core (Fig. III-6). A trend line was overlaid to better infer the underlying gradients. The trend lines show the average variation of the sample scores. Along axis 1 three groups were distinguished, with zones 1 and 2 forming one group (with similar scores and variability) and zones 3 and 5, and zone 4 forming the other two groups. Inferred nutrient levels or trophic state (based on species distributions on this axis) increase towards the left on axis 1. Nutrient levels were inferred to increase after *ca.* 6700 years BP. This corresponded to when *F. construens* v. *venter* replaced *Cyclotella pseudostelligera*, and benthic species became dominant (zone 3). After *ca.* 4300 years BP, *Aulacoseira ambigua* became dominant which suggested a further increase in trophic state. *F. construens* v. *venter* regained dominance after *ca.* 2700 years BP, and a decrease in nutrient status was inferred with conditions being similar to those in zone 3. Nutrient concentrations were related to changes in both species composition and community structure, since both dominant species, and dominant community type were affected.

Along axis 2, two groups were distinguished. Zones 1, 4 and 5 formed one group, while zones 2 and 3 formed the other group (Fig. III-6). Inferred gradients along this axis were water turbulence and water depth. These increase towards the right and left on the axis, respectively. Fluctuations in water levels and/or water clarity, as suggested by the oscillations between planktonic and benthic dominance, ended *ca.* 7500 years BP. Small *Cyclotella* species and long, delicate *Fragilaria* species began to dominate at this time. Based upon the excellent preservation of *F. nanana* and *F. tenera*, water turbulence decreased, and perhaps water clarity and water depth, increased. Between *ca.* 7500 to 4300 years BP, water turbulence gradually increased, while water depth gradually decreased. Turbulence was high, while water depth and clarity were low *ca.* 4300 years BP. Growth of *Aulacoseira ambigua* benefits from turbulent water, as this heavy species requires turbulence to remain in the photic zone (Lemmen *et al.*, 1988). After *ca.* 4300 years BP up to the present, turbulence, and possibly water depth began to gradually decrease and increase, respectively.

The groups distinguished by DCA axis 1 (zones 1 and 2; 3 and 5; 4) had a similar community structure, either benthic or planktonic dominance, whereas groups along DCA axis 2 (zones 1; 4 and 5; 2 and 3) did not. Change on the inferred gradient along DCA axis 1 influenced not only species succession but also community structure. High nutrients favor some planktonic species. When they decrease, planktonic populations typically decrease. Depending upon the initial plankton population size, a decrease in a planktonic population may lead to a clearer water column and better illumination of the sediments. This will favor benthic species. Also, slight variations in total amount of nutrients available, or ratio of available essential nutrients (e.g., phosphorus to nitrogen; silica to phosphorus) will affect species succession (Kilham *et al.*, 1996). The gradient along DCA axis 2 influenced only species succession. Some planktonic species are highly silicified and can tolerate abrasion by particles, while others are lightly silicified and will easily break under too much friction. The gradient of water turbulence could result in a succession of species.

III.E. Conclusions

The diatom record from Mariana Lake suggests that the lake has always been relatively shallow, but that changes in the lake can be linked to climate and the catchment. *Fragilaria* and *Cyclotella* species co-dominated from *ca.* 9100 to 7500 years BP. Water depth was inferred to have fluctuated during this interval. Lake production or trophic state was inferred to have been similar from *ca.* 9100 to 6700 years BP (Fig. III-6 & III-7). Over the same period, water turbulence and water depth were inferred to have decreased and increased, respectively. Inferred turbulence decreased dramatically *ca.* 7500 years BP. Between *ca.* 7500 to 6700 years BP small *Cyclotella* species and long fine pennate species (*Fragilaria nanana* Lange-Bertalot and *F. tenera* (W.Smith) Lange-Bertalot) dominated. The Holocene climatic optimum in central Alberta was estimated to have occurred between *ca.* 9300 and 5600 years BP (Schweger, 1987), but between *ca.* 8000 to 7000 years BP in the Mariana Lake area (Nicholson & Vitt, 1990). The excellent preservation of long, fine pennate diatoms does suggest low water turbulence, and indirectly this could be related to a warmer, more stable climate, stabilized soils, decreased erosion and less material introduced into the lake. Diatom evidence indicated that this occurred between *ca.* 7500 to 6700 years BP. This is similar to the timing of the Holocene thermal optimum inferred from the peatland record (Nicholson & Vitt, 1990). Low nutrient concentrations were inferred for the entire interval from *ca.* 9100 to *ca.* 6700 years BP.

A major change in lake production was inferred *ca.* 6700 years BP. Maximum Holocene aridity at Mariana lake was interpreted from highest abundance of *Populus* pollen between *ca.* 7500 to 5500 years BP, and the near disappearance of *Sphagnum* spores between *ca.* 9000 and 6000 years BP (Hutton *et al.*, 1994). Lake nutrient concentrations are inferred to have increased, but this was a delayed response to the Holocene optimum and peak *Populus* populations. Also, by *ca.* 6700 years BP, turbulence was inferred to have increased. By *ca.* 4300 years BP both water turbulence and nutrient concentrations were inferred to have increased. It was between *ca.* 4300 to 2700 years BP that the lake was suggested to be the most productive and turbulent (by the dominance of *Aulacoseira ambigua*). Lake turnover introduced nutrients into the water column (from the sediments), and thus increased lake nutrient concentrations.

Extensive paludification of the Mariana lake catchment occurred from *ca.* 5000 to 2000 years BP (Nicholson & Vitt, 1990), while the uplands experienced only minor changes. These fluctuations caused changes in the lake. Increased lake production and changes in the diatom assemblages were related to catchment events and indirectly to climate.

Finally, after *ca.* 2700 years BP lake production was inferred to have declined abruptly, and then finally leveled off. Lower lake nutrient concentrations, perhaps lower water levels, and increased water transparency occurred. Through paludification, the upland is gradually replaced by wetland. After *ca.* 2700 years BP more of the catchment was wetland which acts as a filter and controls the amount of water entering the lake. Thus low lake nutrient concentrations were suggested over the last *ca.* 2700 years. Through the used of diatoms as proxy indicators, the lake has been relatively stable since *ca.* 2700 years BP. Much of the landscape, and many other lakes across Alberta were also stable by this time.

This study illustrated that Mariana Lake responded differently than lakes to the north and south to Holocene climate. Variations in climate on a spatial and temporal scale have to be considered. A middle Holocene drought period, *ca.* 7500 to 4000 years BP (Vance, 1986b), was interpreted at Mariana Lake between *ca.* 7500 to 5500 years BP (Hutton *et al.*, 1994). Estimated thermal optimum during the middle Holocene had varying effects on lakes and the landscape along a latitudinal scale due ultimately to variations in climate intensity along the same scale (Vance *et al.*, 1995). Compared to Mariana Lake, the effect of a warmer climate on a more northerly lake did not cause decreased water or nutrient levels due to evaporation (Chapter II), while in a more southerly lake it caused saline species to dominate (Hickman & Schweger, 1996). This and other studies illustrate that lakes and vegetation in the middle of a large ecoregion are variable over time. These sites still show development and change over the post-glacial period. It is interesting that the last pollen zone (*ca.* 5500 years BP to the present) determined by Hutton *et al.* (1994) corresponded to two inferred diatom zones. Insignificant changes occurred in the upland vegetation, while clear and distinct changes occurred within the lake. To further investigate other sites within this very large ecoregion, many types of bioindicators, such as diatoms, algal pigments, pollen and animals should be used. This study showed that even within the large mosaic of the Boreal Forest, that lakes have been changing over the post-glacial period. Lake biota are often influenced by changes in the catchment.

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Table III-1. A summary of major vegetation changes and inferences. Adapted from Hutton *et al.* (1994).

^{14}C years BP	Pollen Zone	Dominant vegetation and inferences
5500 to present	5	*Pinus-Picea* Approaching modern vegetation by *ca.* 2800 Peatlands established by *ca.* 3000 to 2000
7500 to 5500	4	*Picea-Betula-Populus* Holocene maximum of *Populus* mixed forest No *Sphagnum* for most of this zone Inferred drier conditions
9000 to 7000	3	*Betula-Picea* *Betula* increased rapidly at *ca.* 9000 Decreased peatlands *Typha* present – fluctuating water levels
10500 to 9000	2	*Picea-Betula* Forest establishment due to climate change or tree migration from the south?
~12500 to 10500	1	*Artemesia*-Gramineae-Chenopodiaceae and Amaranthaceae Sparse pioneering vegetation

Table III-2. Radiocarbon dates from Mariana Lake (from Hutton *et al.*, 1994)

Depth (cm)	Material	(radiocarbon years) ^{14}C age
203 – 209	gyttja	2780 ± 130
402 – 410	gyttja	4140 ± 110
502 – 508	gyttja	5290 ± 110
605 - 610	gyttja	7660 ± 110
649 – 655	gyttja	8850 ± 90
695 – 700	clayey gyttja	11,300 ± 110

Table III-3. List of some of the diatom species found in the Mariana Lake core. These species were used in the statistical analysis.

Number	Species Name
1	*Achnanthes conspicua* Mayer
2	*A. exigua* Grunow
4	*A. lanceolata* (Brébisson) Grunow
5	*A. laterostrata* Hustedt
6	*A. linearis* (W. Smith) Grunow
7	*A. minutissima* Kützing
9	*A. suchlandtii* Hustedt
13	*Amphora pediculus* (Kützing) Grunow
16	*Anomoeoneis vitrea* (Grunow) Ross
19	*Aulacoseira ambigua* (Grunow) Simonsen
21	*A. granulata* (Ehrenberg) Simonsen
22	*A. italica* (Ehrenberg) Simonsen
29	*Cocconeis placentula* Ehrenberg
30	*Cyclotella distinguenda* Hustedt
33	*C. pseudostelligera* Hustedt
35	*C. stelligera* Cleve & Grunow
39	*Cymbella cessatii* (Rabenhorst) Grunow
42	*C. microcephala* Grunow
43	*C. minuta* Hilse
44	*C. ventricosa* Agardh
59	*Eunotia incisa* Gregory
69	*Fragilaria brevistriata* Grunow
70	*F. capucina* Desmazières
74	*F. construens* (Ehrenberg) Grunow *v. construens*
76	*F. construens* (Ehrenberg) Gruonw *v. venter*
82	*F. nanana* Lange-Bertalot
85	*F. pinnata* Ehrenberg
86	*F. tenera* (W. Smith) Lange-Bertalot
94	*Gomphonema gracile* Ehrenberg
96	*G. minutum* (Agardh) Agardh
97	*G. parvulum* (Kützing) Kützing
98	*G. truncatum* Ehrenberg
105	*Navicula cryptotenella* Lange-Bertalot
108	*N. elginensis* (Gregory) Ralfs
110	*N. harderii* Hustedt
114	*N. minima* Grunow
115	*N. laevissima* Kützing

Table III-3. Continued.

116	*N. lanceolata* (Agardh) Ehrenberg
117	*N. leptostriata* Jørgensen
120	*N. pseudoventralis* Hustedt
121	*N. pupula* Kützing
122	*N. radiosa* Kützing
125	*N. seminulum* Grunow
148	*Stauroneis anceps* Ehrenberg
151	*Stephanodiscus hantzschii* Grunow
153	*S. parvus* Stoermer & Håkansson
156	*Tabellaria flocculosa* (Roth) Kützing strain IV *Sensu* Koppen
157	*T. flocculosa (Roth) Kützing strain IIIp Sensu* Koppen
158	*Achnanthes subatomoides* (Hustedt) Lange-Bertalot & Archibald
160	*Cyclotella ocellata* Pantocsek
161	*C. stelligeroides* Hustedt
162	*Navicula cf. submuralis Hustedt*
163	*Gomphonema subtile* Ehrenberg
164	*Navicula cryptocephala* Kützing
165	*N. subrotunda* Hustedt
166	*N. sublucidula* Hustedt

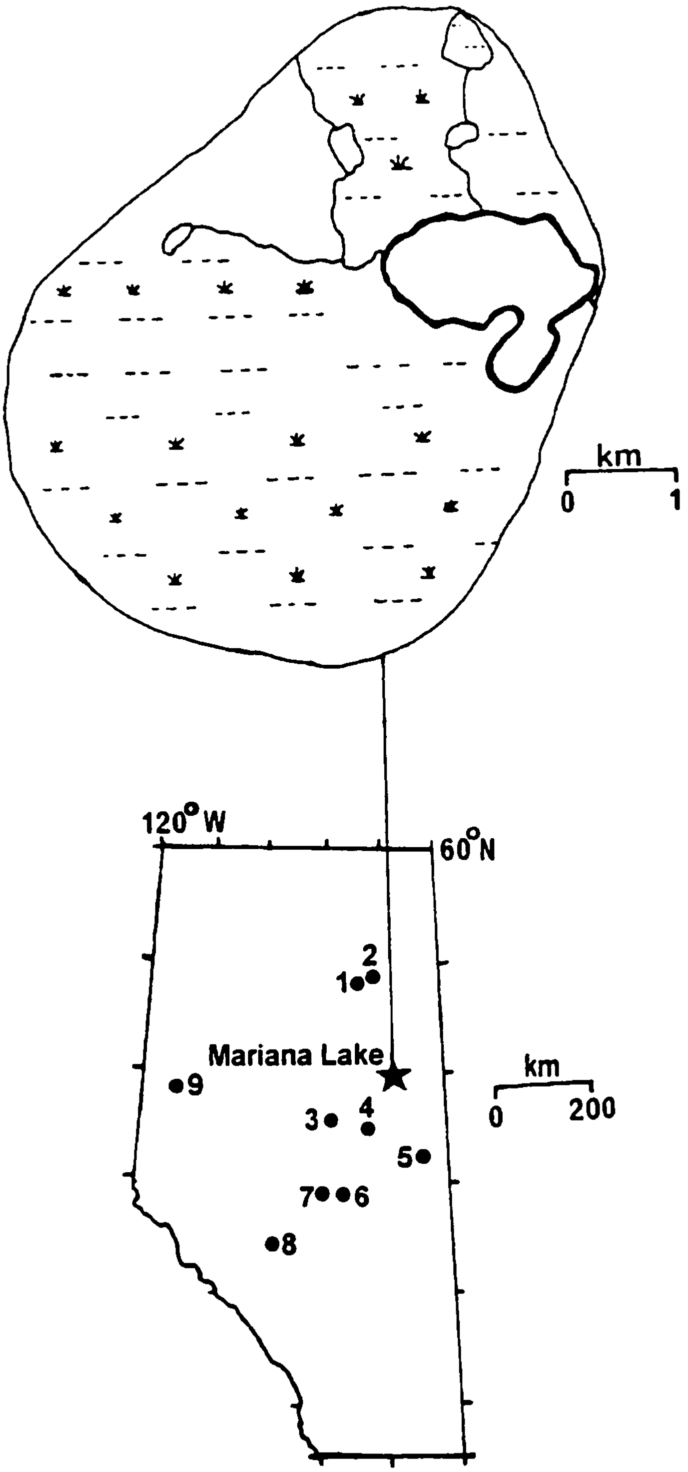

Figure III-1. Map of Alberta indicating the location of Mariana Lake (★). Also indicated are the locations of other sites referred to in the text (1=Otasn Lake; 2=Eaglenest Lake; 3=Baptiste Lake; 4=Lofty Lake; 5=Moore Lake; 6=Smallboy Lake; 7=Lake Wabamun; 8=Fairfax Lake; 9=Spring Lake).

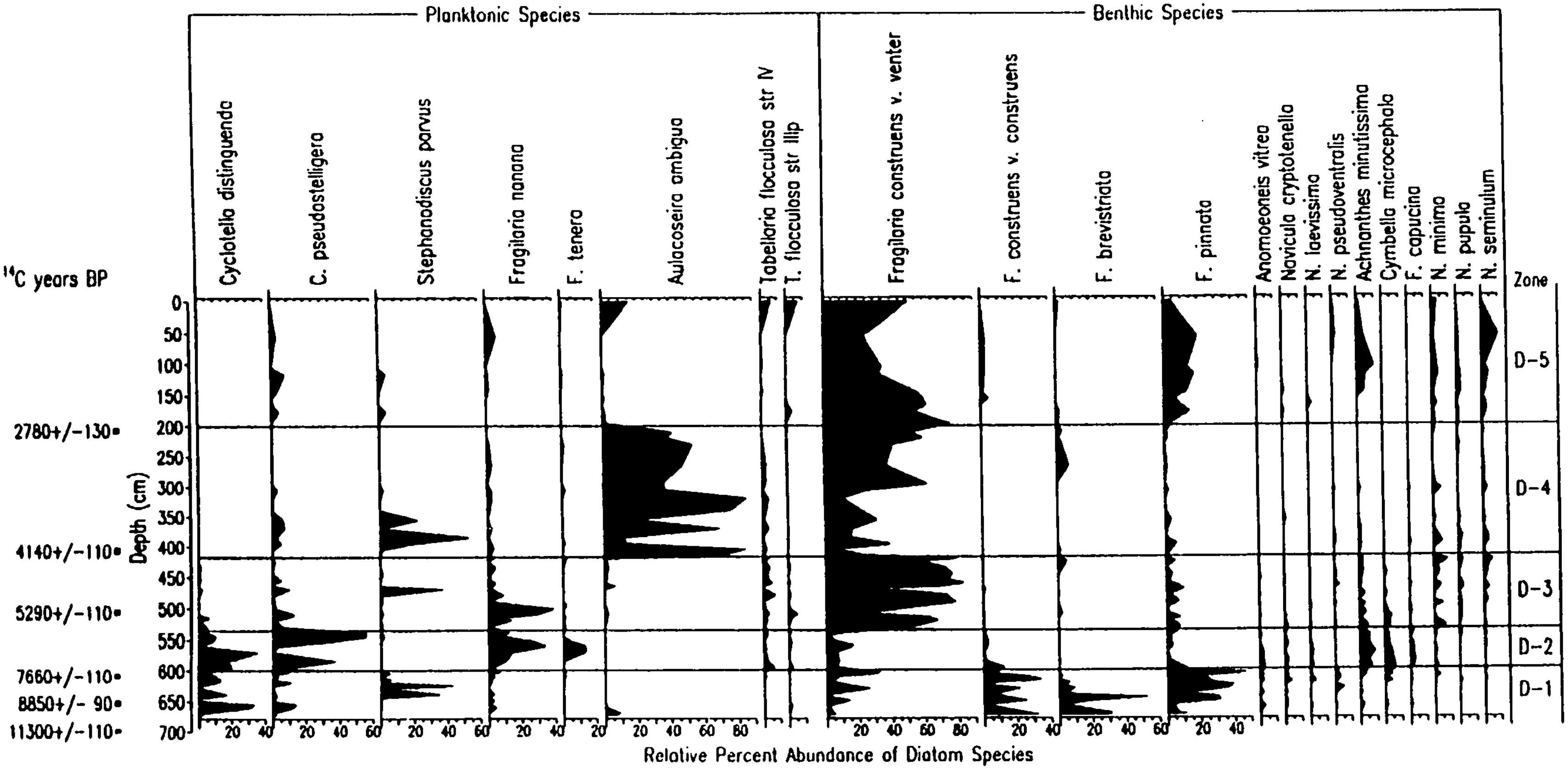

Figure III-2. Summarized species stratigraphy for Mariana Lake. Values are relative percent abundance of total diatom count. Only those species in at least 10 samples at more than 3 % relative abundance were included.

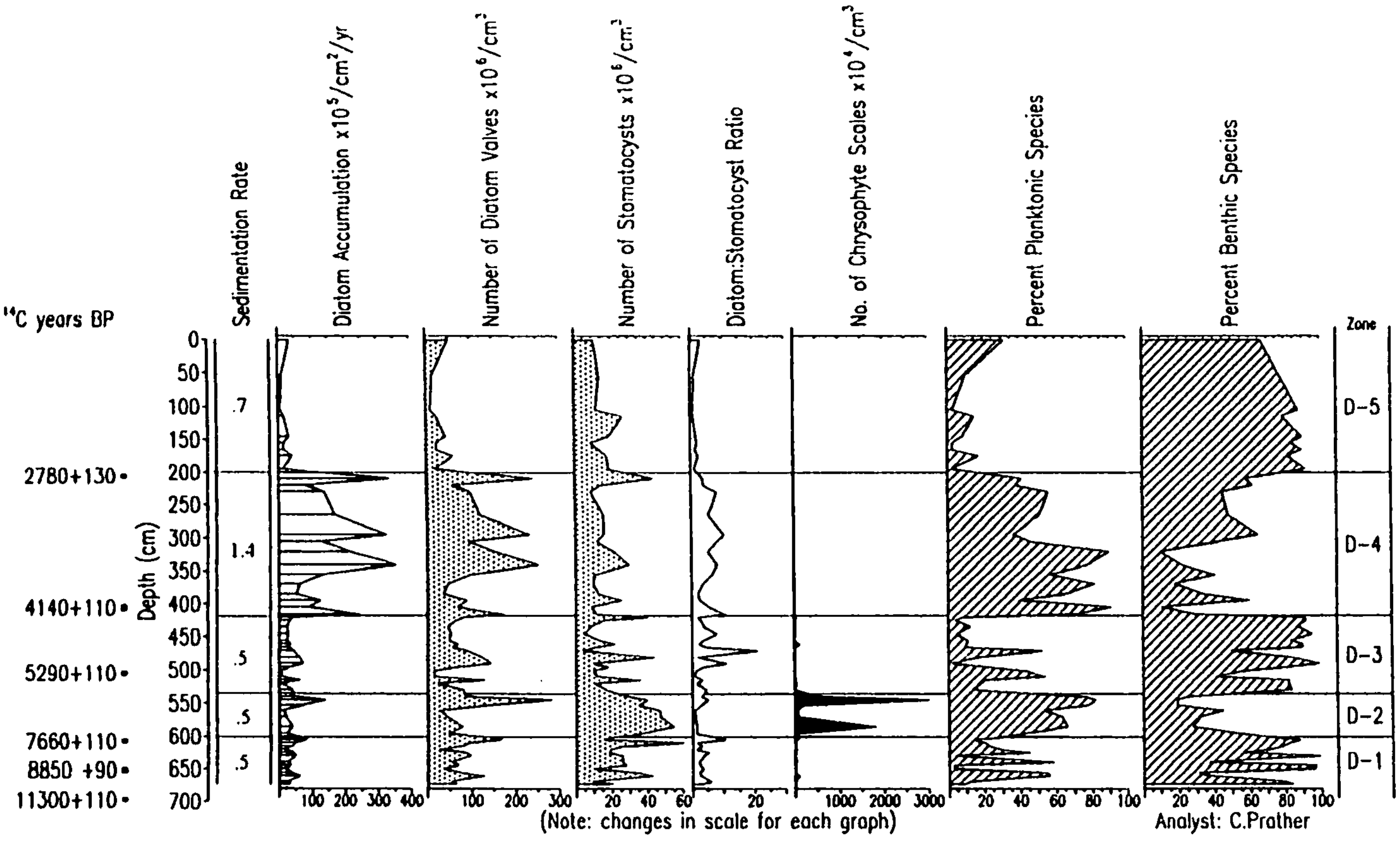

Figure III-3. Summary of total diatom valves, chrysophyte stomatocysts and scales found in the Mariana Lake core. Diatom numbers are presented as accumulation (x10^6 /cm^2/yr) and concentration (x10^6/cm^3), while stomatocysts and scales are only presented as concentration (x10^6/cm^3 and x10^4/cm^3, respectively). Total number of valves of planktonic and benthic species as a percent of total valves were calculated.

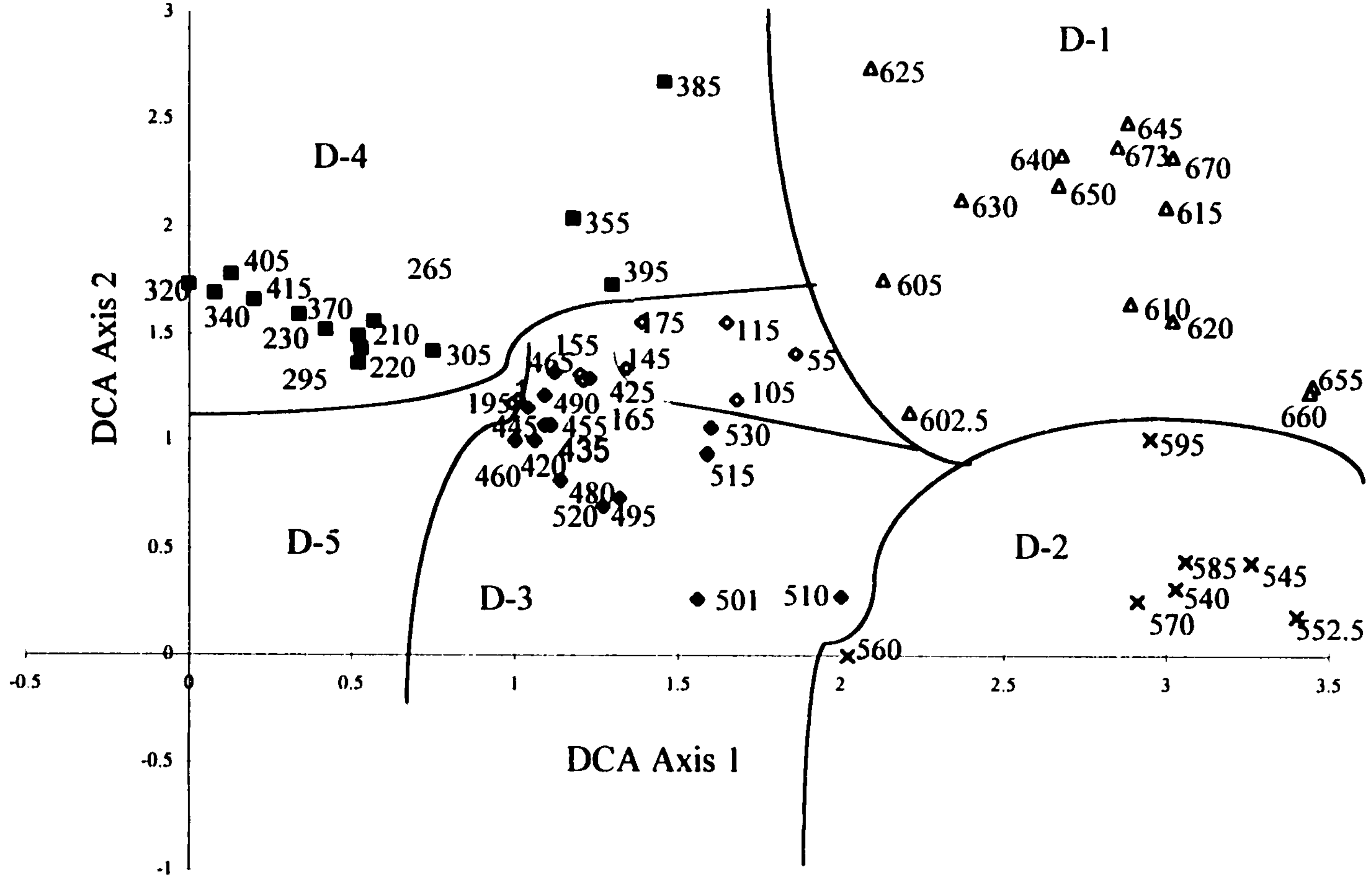

Figure III-4. Detrended Correspondence Analysis (DCA) results for the samples from the Mariana Lake core. Samples are divided into 5 stratigraphic zones [(Δ) zone 1, (x)zone 2, (◆)zone 3, (■)zone 4, (◇)zone 5].

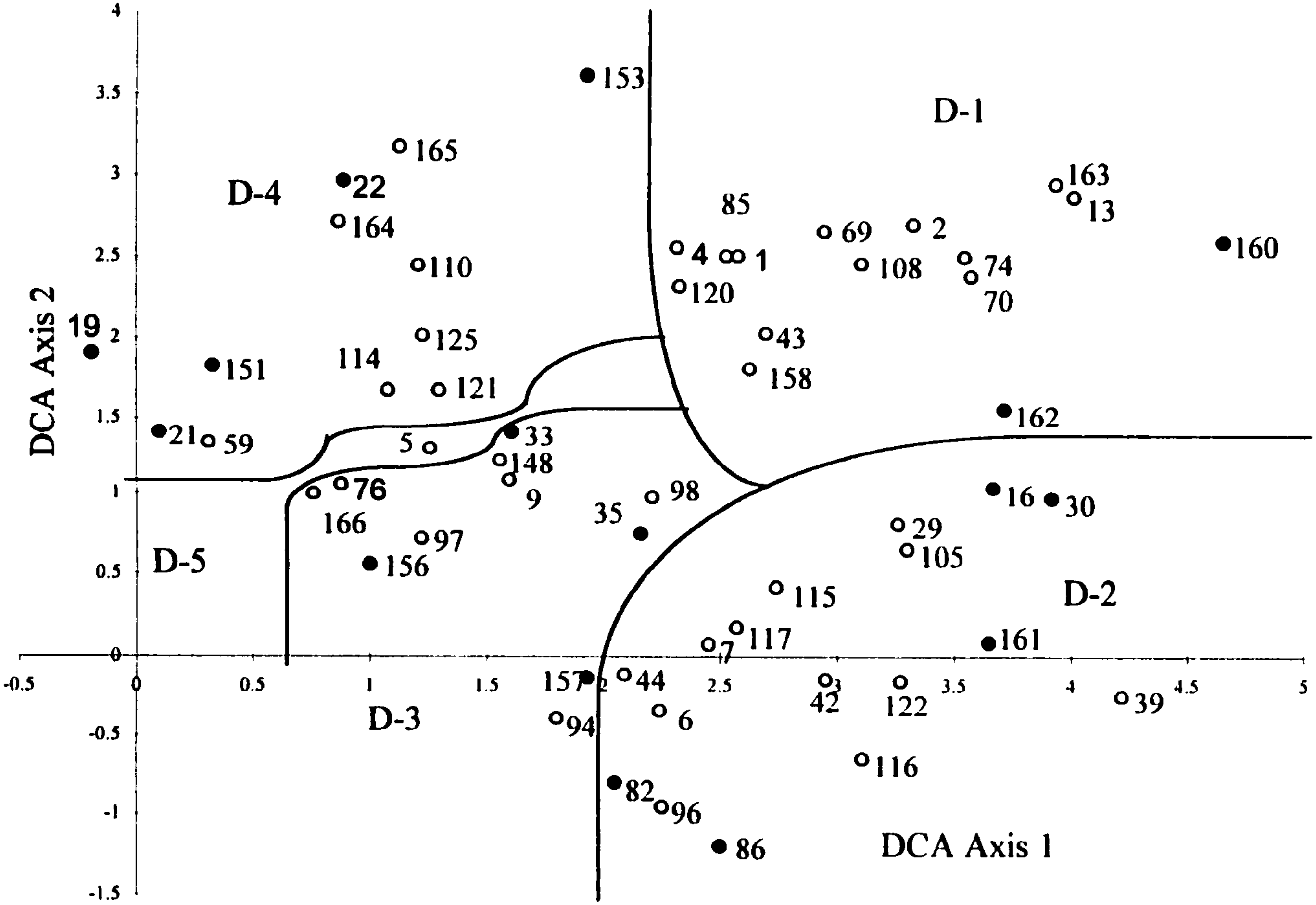

Figure III-5. Species scores from the DCA. Species are divided into the 5 stratigraphic zones. Symbols indicate if the species is a main component of the plankton (●) or of the benthos (o). Corresponding species names are given in Table III-3.

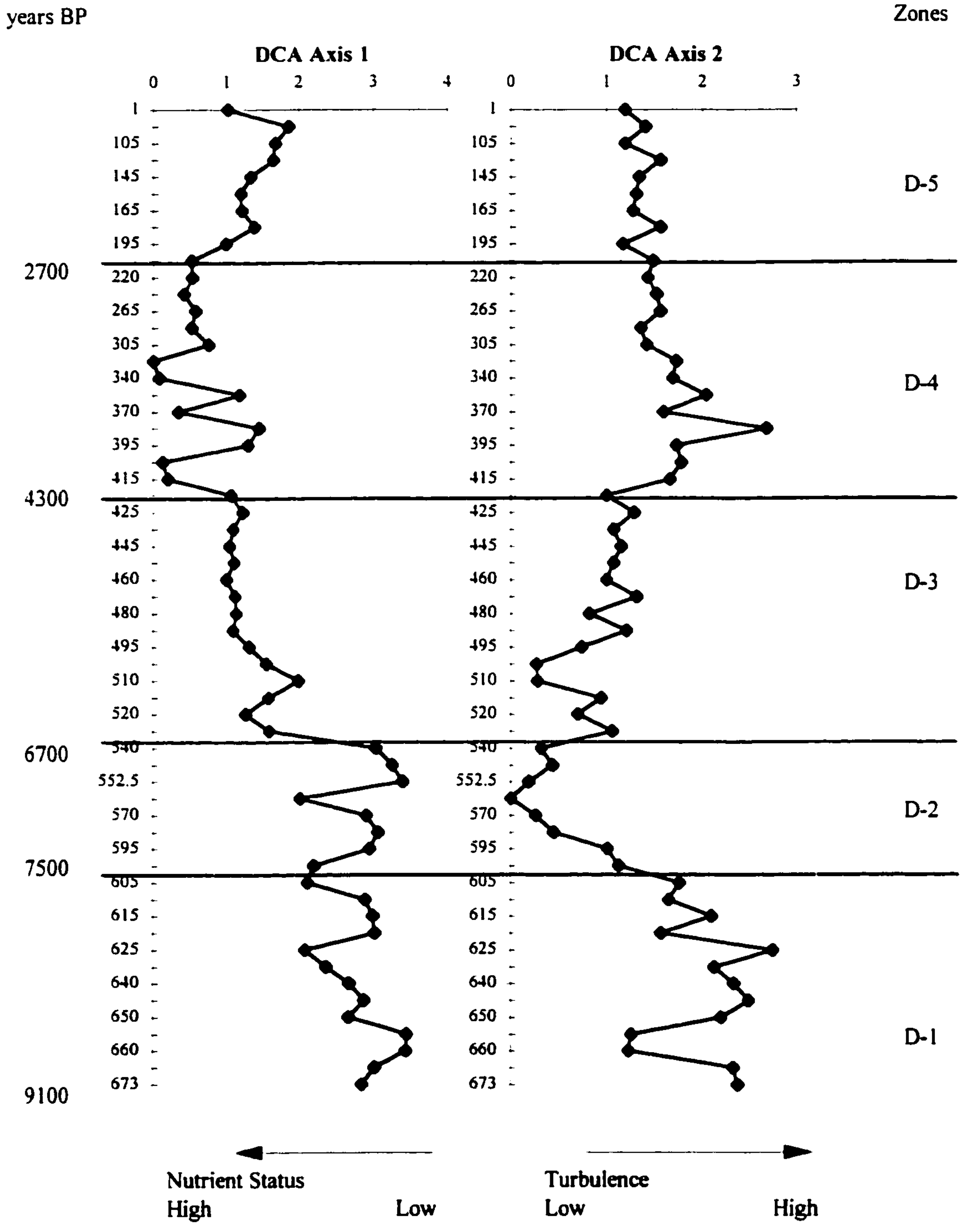

Figure III-6. Sample scores from the Detrended Correspondence Analysis plotted versus depth in the core. Stratigraphic zones, with approximate time boundaries are indicated. Inferred gradients on axis 1 (nutrients) and on axis 2 (turbulence and water depth) are indicated.

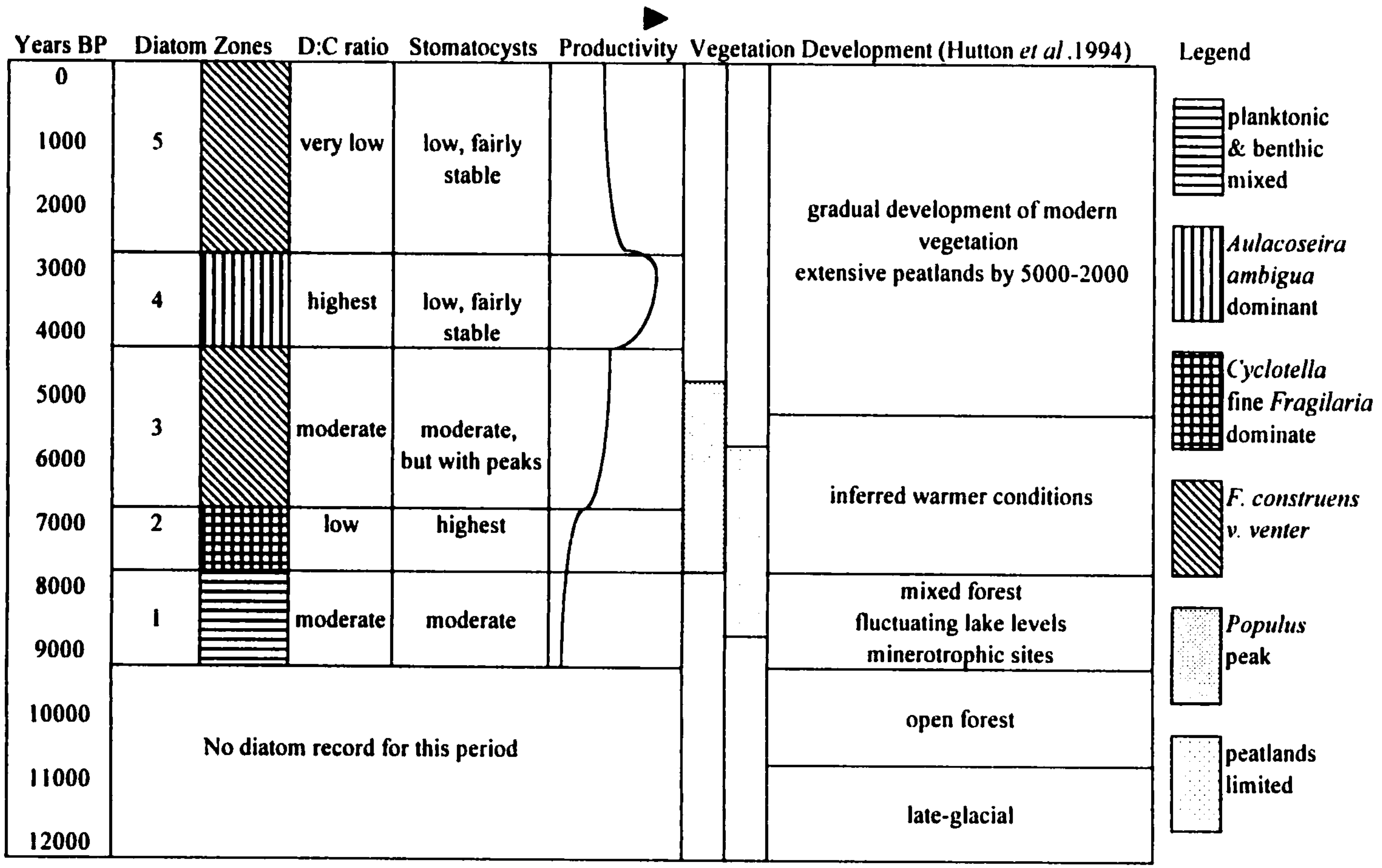

Figure III-7. Summary of changes in diatom and chrysophyte (D:C ratio) remains from Mariana Lake. Diatom zones with inferences of changes in lake productivity are given. Vegetation zones with catchment inferences adapted from Hutton *et al.* (1994).

Chapter IV. A survey of the modern sedimentary diatom assemblages from 80 Alberta lakes and the relationship to water chemistry.

IV.A. Introduction

Management of lakes is currently a prime topic due to the concern of human impact upon lakes, and the decline in water quality as measured through chemical and biological analyses. Epilimnetic total phosphorus (TP) concentration are used to determine the trophic level (oligotrophic, mesotrophic or eutrophic) of a lake (Forsberg & Ryding, 1980; Yang & Dickman, 1993). Algal analyses are also used to determine trophic status (e.g., Nygaard, 1949) by determining species composition, or concentration of chlorophyll *a* [which is an indication of phytoplankton blooms (Evans & Prepas, 1996)] and standing crop (Hickman & Klarer, 1975).

Algal habitats range from lakes and streams to aerial substrata (e.g., rock faces, plants and fungi) (Round, 1981). Algae can grow on and in rocks, sediments and plants, and within the water column. Due to the microscopic nature of algae, the algal communities are defined by the substratum with which they are associated. This study divided diatom species into components of the plankton (free-floating in the water column) or the benthos (associated with a substrate).

Diatoms are a major component of the phytoplankton, and the attached algal communities (epipelon, epiphyton and epilithon) (Wetzel, 1975; Lee, 1989). They are sensitive to various environmental factors. Early studies established the relationship between diatom species and salinity (Kolbe, 1927), pH (Hustedt, 1937-39), and sediment organic matter and calcium content (Round 1957a & 1957b). Other studies demonstrated that the abundance of individual planktonic diatom species changed along a trophic gradient (Round & Brooks, 1959), and that the abundance of individual epipelic species changed along a gradient of calcareous to acidic lakes (Round, 1959).

Diatoms are known to undergo seasonal succession (e.g., Round, 1960, 1972; Hickman 1976, 1982; Hickman & Klarer, 1974). Species succession is related to environmental factors such as temperature, light availability, silica and other required elements in the water and sediments (Lee, 1989). Using multivariate statistical analyses, environmental variables that significantly influence diatom species distributions have been identified. Relations between diatoms and a number of environmental variables have been described, e.g. pH (Charles, 1985; Dixit, 1986; Birks *et al.*, 1990; Charles *et al.*, 1990; Dixit *et al.*, 1991), salinity (Fritz, 1990; Fritz *et al.*, 1991; Cumming & Smol, 1993; Wilson *et al.*, 1996), dissolved organic carbon (Pienitz & Smol, 1993), TP (Hall & Smol, 1992; Fritz *et al.*, 1993; Reavie *et al.*, 1995), water depth (Yang & Duthie, 1995) and water temperature (Pienitz *et al.*, 1995). These relationships were determined by analyzing the surficial sedimentary diatom assemblages of many lakes along a gradient of the environmental variable. Usually 30 to 60 lakes from one region are chosen to form a data set (Dixit *et al.*, 1992) through analysis of their surficial sedimentary diatom assemblages. In the surficial sediments there lie a mixture of the various diatom species that lived in all habitats of the lake over the last few years (Dixit *et al.*, 1995). The surficial sediments represent spatial and temporal diatom assemblages mixed together. Epilimnetic water from these lakes is analyzed for chemical variables such as pH and concentration of TP, calcium, magnesium and dissolved organic carbon. In addition, physical factors such as water depth, water temperature, lake area and watershed area may also be measured. Through multivariate statistical analyses, the relationship between diatom species and these chemical and physical variables of the lakes are determined. Species responses to a selected environmental variable are determined, an inference model for this variable is derived, and then this model is applied to other assemblages of species to estimate the variable at other sites, or times (Duff & Zeeb, 1995). These data sets may also provide information about species distributions over wide areas (by comparing various data sets), information about species diversity in specific regions, opportunity to compare lake water chemistry between regions, and insight into the ecology of many species.

In central Alberta there have been some detailed studies done on diatom succession (e.g., Hickman 1976, 1978, 1979, 1982; Hickman & Klarer, 1974; Zhang & Prepas, 1996). These studies analyzed algal species succession and population succession (i.e., Bacillariophyceae, Chlorophyta, Cyanophyta, etc.) from a few lakes over multiple years. A survey of Alberta lakes has been done which included information on lake morphometry, vegetation catchment, lake chemistry, and occasionally lake biota (Mitchell & Prepas, 1990). Most of the lakes surveyed by Mitchell and Prepas (1990) are located in central to southern Alberta. There is no complementary survey for lakes from northern Alberta, yet lakes abound within the northern region of the province.

There has been no comprehensive investigation of the diatom assemblages from the lakes in Alberta. This study was undertaken to analyze the diatom species diversity in these lakes, and examine the relationship of species to lake chemical and physical variables. Sites were chosen randomly and did not follow a predefined gradient, since this was an investigation to determine diatom biodiversity in Alberta lakes. The primary objectives of this investigation were to document the surficial sedimentary diatom assemblages in lakes of northern and central Alberta, and to examine relationships between the diatom assemblages and measured environmental variables. In data sets generated to study a specific variable, the significant influence of the variable upon diatom species distribution was determined. Diatom species distributions are influenced by pH (and related components), salinity, trophic variables, and dissolved organic carbon. In these previous data sets, lakes are chosen to fit within a specific range of each predefined variable. It was hypothesized that species distributions would still be strongly influenced by environmental variables even though the lakes in this data set were not selected to follow a predefined gradient.

IV.B. Site Description

The province of Alberta can be divided into several ecoregions. They are defined primarily by geographic and climatic features (Crosby, 1990) because these influence the vegetation and soils that develop in an area. The ecoregions of Alberta have been mapped and described by Strong and Leggat (1981). They defined 12 ecoregions. Four of these ecoregions are shown, along with the location of the 93 lakes used in this study (Fig. IV-1).

Location of climate stations (Fig. IV-1) and detailed information for each station is given (Table IV-1). These values are based on 30-year climate normals (Atmospheric Environment Service, 1993). Annual total precipitation (mm) (Fig. IV-2a) and mean July temperature (° C) (Fig. IV-2b) for the province have been summarized (Atlas of Alberta, 1984). The annual total precipitation in the northern to central regions is generally higher than in the southern regions. Northern Alberta, along with mountain and foothills regions, experience cooler summer temperatures than the southern portion of the province. As a result dense forest tends to develop in the northern, mountain and foothills regions, open parkland to grasslands tend to develop in the central region, and dry grassland tends to develop in the southern region (Fig. IV-1).

The Boreal Forest region of Canada (Rowe, 1972) occupies approximately the northern two thirds of the province, and has been divided into five ecoregions by Strong and Leggat (1981). Much of the vegetation of the Boreal Forest consists of trees including *Betula balsamifera, Populus tremuloides, Pinus banksiana, Picea glauca,* and *P. mariana*. The importance of each tree species in the catchment of a lake is influenced in general by precipitation, evaporation and soil type. Wetlands and peatlands also occur in the Boreal Forest region, and in some areas, open peatlands, as opposed to dense forests, occur over large areas (Halsey *et al.*, 1997). The Montane Boreal Forest typically has *Pinus banksiana, Picea glauca*, and *P. mariana* as the dominant tree species. Finally, the Aspen Parkland typically has *Populus tremuloides* as the only tree species. The remaining area is usually occupied by grass species. This area is typically drier, due to more evaporation than the more northerly Boreal Forest. In addition decomposition rates are generally higher, thus limiting moss accumulation (Zoltai & Vitt, 1990). The stands of trees in the Aspen Parkland can vary from dense forests in the northern and western regions, to open groveland in the southern and eastern portions. This ecoregion is variable in runoff, and as a result lake levels can vary from year to year (Crosby, 1990).

Lakes used in study occur in three of the five Boreal Forest ecoregions, and from two other ecoregions of the province (Fig. IV-1). The geographical locations of some areas in Alberta discussed in the text are given. From the Birch Mountain area of Northeast Alberta (57° to 58° 10^{1}N; 112° to115° W) and east to the Alberta border, 34 lakes (1-34) were sampled. Four lakes (63-66) located on the Canadian Shield in the northeast corner of the province (59° to 60° N; 110° to 111° W) were sampled. From the Caribou Mountains area of far north-central Alberta (58° 45^{1} to 60° N; 114° 17° to116° 50^{1} W), 12 lakes (35-44, 67 & 68) were sampled. South of the Caribou Mountains is an area known as the Buffalo Head Hills (56° 30^{1} to 58° 13^{1} N; 115° 30^{1} to117° W). Twelve lakes in and to the west of this area (45-56), plus another 3 (57-59) at the Alberta/British Columbia border were sampled. From the Montane Boreal Forest region (54° 30^{1} N; 119°

50^{1} W), 3 lakes (60-62), and 2 more lakes north and east of the area (87 & 88) were sampled. In central Alberta, near the transition of the Boreal Forest-Aspen Parkland ecoregion and near the southern boundary of the Aspen Parkland, 23 lakes (69-93) were sampled. In some studies a specific environmental variable is chosen and then lakes are selected to fit within a specified range of that variable. Lakes in this study were not chosen to meet specific requirements, but rather they were selected as a representation of lakes in Alberta.

The algal assemblages of two closely adjacent lakes from the same ecoregion can be quite different. Differences may be due to internal or external lake factors. External influences may include catchment size, elevation, groundwater aquifers, degree and type of anthropogenic impact in a catchment, and direct impacts on a lake. These factors were not measured or accounted for in this study, and they could in fact have significant influences upon the diatom assemblages, and on the species relationship to the physical and chemical parameters of the lake.

IV.C. Methods

IV.C.1. Sampling

The lakes included in this study were sampled by personnel of Alberta Environment (n=87) and the Limnology Lab, University of Alberta (n=6). Samples for surficial sediments and water chemistry were taken from the deepest part of each lake. Lakes were sampled once during August 1992 (n=56), August 1993 (n=12), and August 1994 (n=19) by personnel of Alberta Environment. Composite water samples for chemical analysis were collected from 0.5 m below the surface of the water, divided into bottles for various analyses, and shipped within 10 hours to the Alberta Environmental Centre for analysis. The uppermost 3 cm of sediment, representing a composite sample of the previous few years, was removed using a Kajak-Brinkhurst (K-B) gravity corer (Glew, 1991). Sediments were placed in plastic containers and stored frozen.

The remaining 6 samples were collected by personnel from the Limnology Lab, University of Alberta at various times. Surficial sediment samples and water chemistry samples were taken once for each lake between June to August 1993. Composite water samples, collected 0.5 m below the surface of the water, were analyzed in the Limnology

Lab. The uppermost 1 cm of sediment was removed from the deepest part of each lake. Sediments were either stored frozen in plastic bags (n=2), or freeze-dried and then stored frozen in plastic bags (n=4).

IV.C.2. Laboratory Analysis

The frozen sediment samples were allowed to thaw slowly, and then 1 cm^3 sub-samples were taken from each and treated with $K_2Cr_2O_7$ and H_2SO_4 to remove all organic matter (Hickman *et al.*, 1984). The diatom slurry was then washed with deionized water until there were no traces of acid. Aliquots of 0.02 - 0.35 mL were pipetted onto cover slips, air dried slowly, and then fixed permanently in Hyrax.

A least 500 diatom valves were counted on each slide at 1000x using oil immersion. Identifications were made using Germain (1981), Hustedt (1930), Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), and Patrick and Reimer (1966, 1975).

The Water Analysis Laboratory at the Alberta Environmental Centre, and the Limnology Lab, University of Alberta analyzed water samples for a variety of chemical variables (Alberta Environment Lab Manual, 1987; Saffran & Trew, 1996). These included pH, specific conductance, alkalinity, total dissolved solids (TDS), and concentrations of dissolved sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), bicarbonate (HCO_3), chloride (Cl), sulphate (SO_4), silica, total phosphorus (TP), and organic carbon (OC). Saffran and Trew (1996) interpreted the water chemistry data from the lakes of northern Alberta.

IV.C.3. Data Analysis

To quantitatively estimate an environmental variable at a site using the species as indicators, estimates of the variable optimum for each species must be known. It is assumed that a species will be most abundant when the site value is close to the optimum value for that species (ter Braak & van Dam, 1989).

The diatom samples came from surficial sediments of each lake. These sediments represent the accumulation of matter over a few years. In order to derive predictive equations it is assumed that the diatom species deposited and preserved in these modern sediments are related to and influenced by the environment of the lake (including the chemistry of the water and morphometry of the basin). Diatom species were tallied as relative percent abundance of total counts in the sample. Diatoms representing ≥ 1% in at least 2 samples were included in statistical analyses.

Chemistry and lake physical data were available for 16 variables. These included maximum water depth (depth), lake area (area) plus the previous 14 chemical variables. Environmental data with a normal distribution is preferred for statistical analysis (Jager & Looman, 1987). Some of the variables had positively skewed distributions and they were ln (x+1) transformed (Zar, 1984). Variables with skewed distributions that were transformed included depth, area, conductivity, alkalinity, TDS, Na, K, Ca, Mg, HCO_3, Cl, SO_4 and TP. The calibration set included 93 lakes, 16 variables and 209 species.

IV.C.3.a. Ordination

Ordination is a statistical method that organizes samples along a hypothetical environmental gradient based upon their species composition (ter Braak, 1987). The computer programme CANOCO (version 3.10) (ter Braak, 1988, 1990) was used to perform the ordinations. Both indirect and direct ordinations were used on the data. Indirect ordination maximizes the dispersion of species along a hypothetical environmental gradient, whereas direct ordination constrains species distributions to measured environmental variables (ter Braak, 1987). Thus, direct ordination, also known as canonical ordination, displays the relationship between species and measured environmental variables. Correspondence Analysis (CA), and the canonical form of CA (CCA), were derived from the weighted averaging method of Whittaker (1967) (ter Braak, 1987). It is based upon the assumption that if a species possesses a unimodal response to an environmental variable it will occur most frequently near the optimum of the unimodal curve (ter Braak and Looman, 1987).

Indirect ordination arranges species along a hypothetical environmental gradient. Detrended correspondence analysis, DCA, is an example of indirect ordination. When using this method it is assumed that species have a unimodal response along environmental gradients (ter Braak, 1987). DCA is useful for data with long underlying gradients (Duff & Zeeb, 1995). DCA estimates lengths of the ordination axes. On long axes (> 3 SD) sites at opposite ends have very few species in common (ter Braak, 1987).

By using this method, samples with unusual species assemblages can be detected, and samples that lie more than 3 SD from the mean of species scores can also be detected. Along the axes, these unusual samples are far removed from all other samples. The remaining samples group together and underlying gradients cannot be inferred. By removing the unusual samples, underlying or apparent environmental gradients can be inferred by indirect or direct ordination, respectively.

CCA is a direct ordination method that also assumes a unimodal response of species to environmental gradients. In canonical ordination the observed environmental variables that can best explain the variation in the species data are determined (ter Braak, 1987). The ordination axes and the site scores are linear combinations of environmental variables (ter Braak, 1987). The result is a maximum of species dispersion. Thus, the pattern of species variation, and the relationship between the species and each environmental variable are displayed on the ordination biplots between species and environmental variables (ter Braak, 1987).

IV.C.3.b. Data Screening

The environmental dataset was examined for unusual samples, repetitive environmental variables, and environmental variables that did not influence diatom species distributions (Birks *et al.*, 1990). The data screening process outlined below follows the methods of Hall and Smol (1992) and Cumming and Smol (1993).

Outlier samples. Samples may have unusual species assemblages or extreme environmental variables. These can influence the results by grouping samples and not showing the underlying gradient in the remaining samples. These samples, called outliers, were removed in order to determine the most influential variables in the remaining samples. The outlier samples were detected by using DCA on the species data. Samples outside of the 95% confidence limits of species scores were deleted from subsequent analyses.

Redundant environmental variables. A variety of steps were taken to remove superfluous environmental variables and reduce the number down to a minimum that would still explain most of the variance in the species data. Environmental variables were included if (1) they were not significantly correlated to other variables, or (2) if they were correlated but they exerted an independent influence on the species data.

To determine superfluous environmental variables the following steps were taken.
(1). Groups of significantly correlated variables ($p \leq 0.05$) were determined from a Pearson correlation matrix.
(2). An initial CCA was run, outlier samples omitted, with the forward selection option. This determined which variables in each of the above groups explained the most variation in the species data. Significance of a variable in explaining species variation was determined through Monte Carlo permutation tests (99 unrestricted permutations; $p \leq .05$). This variable was used as a representative of the group.
(3). To determine if any other correlated variables of a single group had independent influence a series of partial CCAs were run. The variable identified in the previous step was chosen as the main variable and each correlated variable was selected individually as the sole co-variable. Independent influence of the co-variable was determined by testing the significance of the first canonical ordination axis ($p \leq 0.05$) using a Monte Carlo permutation test with 99 unrestricted permutations. Only those variables with significant influence were retained for further analyses.
(4). Another CCA was run on the dataset with outlier samples and non-significant variables excluded. At this stage variables with high variance inflation factors (VIF > 20) were identified. These variables have unstable coefficients and do not merit further interpretation (ter Braak, 1986). A series of CCAs were run omitting the variable with the highest VIF in each run until all variables had VIF values less than 20.

After all non-significant variables were removed, the results were checked for extreme samples. Extreme samples may also have unusual diatom assemblages and/or unusual values of environmental variables (Birks *et al.*, 1990), which could bias the results. These samples were not detected as outliers using DCA. Samples which have extreme values for any environmental variable are identified by a large influence (> x5) in the CCA output (Birks *et al.*, 1990). Any sample with an extreme influence in 1 or more environmental variable was deleted from the final CCA.

A final CCA was run once all outlier samples, non-significant environmental variables, and extreme samples were removed. Forward selection was used to determine the significance of each variable and the amount of variation explained by each variable.

IV.D. Results

IV.D.1. Data Screening

The original data set consisted of 93 lakes and 16 environmental variables. A list of the 93 lakes and values for some of the important environmental variables are given (Table IV-2). A summary of the 10 environmental variables and the 80 lakes used in the final CCA are also given (Table IV-3).

After the surficial sediment samples were analyzed for diatom species composition (209 diatom species were identified), the data set was statistically analyzed to determine if there were any patterns in the data, and if the species distributions were influenced by any environmental variables.

Before statistical analysis, samples 89, 90 and 91 were removed because they had incomplete environmental data. Also, two variables (dissolved silica and dissolved organic carbon) were removed because values were not available for every sample. These three samples and two environmental variables were removed from subsequent analyses.

Species with more than or equal to 1% abundance in at least two samples were included in the statistical analyses. DCA was used to detect any outlier samples. Outlier samples were those with unusual species assemblages and/or extreme environmental variables. Three samples were outside of the 95% confidence limits (2 SD) of the mean species scores and were omitted. Sites 14 (L29), 54 (L96), and 82 (Buffalo Lake) were identified as outliers. Sample 14 had an extreme environmental variable (pH = 4.5) while sample 54 had a very high occurrence of *Gomphonema angustatum* (92) (55%) (numbers in parentheses following diatom species refer to species numbers in Table IV-5; Fig. IV-4 & 5). This species was otherwise rare in any other lake. Finally, sample 82 had both extreme environmental variables (very high dissolved solids and ions), and a very high occurrence of *Fragilaria capucina* v. *mesolepta* (71) (> 85%). Once these three samples were removed no other samples were identified as outliers. These three samples were removed from all subsequent analyses.

The described data screening process was applied to the remaining 87 lakes and 14 environmental variables to determine the most important variables in the data set, and to determine which variables significantly influenced the diatom species composition in these lakes. A CCA was run to determine groups of significantly correlated variables. TP was the only variable that was not significantly correlated to other variables. The other 13 variables had significant correlations to at least one other variable. These formed groups of significantly correlated variables. Forward selection was used to determine which variables explained a significant ($p \leq 0.05$) amount of the variation in the diatom species data. Water depth, TDS, TP, and lake area were the only variables that were significant. These four variables were used individually in partial CCAs to determine if correlated variables also explained significant variation. For example, forward selection identified water depth as significant. It was then used as the sole variable in a series of partial CCAs. In each partial CCA, a significantly correlated variable was used as the sole co-variable. If it did not exert significant influence it was removed from further analyses. In this example, lake area was a co-variable, and it exerted significant influence upon species variation. Lake area was retained in further analyses.

Following these steps, two variables (alkalinity and sodium) were removed due to insignificant influence ($p > 0.05$). The variables of conductance and TDS were also removed due to high variance inflation factors ($VIF > 20$).

Extreme samples were then detected in the data set. Samples 13, 47, 56, 73, 78 85 & 92 had extreme influence (> x5) in at least one environmental variable. Sample 13 had a low pH (5.28). Sample 47 had a very low concentration of bicarbonate (0 mg HCO_3/l), but high concentrations of chloride (28 mg/l) and sulphate (582.96 mg/l). Sample 56 had a very low concentration of calcium (0 mg/l), sample 73 had high concentrations of potassium (26.8 mg/l) and magnesium (115 mg/l), and sample 85 was very deep (60 m). Samples 78 and 92 had unusual species and environmental variable combinations. In sample 78, very high TP concentration (330 µg/l) and very high abundance of *Fragilaria crotonensis* (77) (34 %) were recorded. Finally, sample 92 was deep (27.5 m) and had a very high abundance of *Stephanodiscus hantzschii* (151) (46 %). A final CCA was run on 80 samples, 10 environmental variables, and 116 diatom species. A summary of these 10 variables across these 80 lakes is given (Table IV-3).

IV.D.2. Ordination

An indirect ordination (Correspondence Analysis; CA) was run on the species data to examine species variation in the samples (results not shown). Eigenvalues derived for the first two axes were 0.601 and 0.493, respectively. These two axes explained a total of 18.7 % of the cumulative percent variance in the diatom data. Direct ordination (CCA) was used on the species and environmental data. Eigenvalues obtained for the first two CCA axes ($\lambda_1 = 0.437$; $\lambda_2 = 0.221$) explained only 11.3 % of the cumulative percent variance in the diatom data, but accounted for 50.6 % of the diatom-environment relationship (Fig. IV-3 & IV-4). High eigenvalues and high correlations between the diatom species and the environmental variables on CCA axis 1 (0.87) and 2 (0.79) indicated that the 10 environmental variables were important in influencing the distribution of diatom species. Both ordination axes were also determined to be significant ($p \leq 0.05$) by a Monte Carlo permutation test with 99 unrestricted permutations. The forward selection option of CCA was used on the data set of 80 lakes to determine which variables explained a significant proportion ($p \leq 0.05$) of the species variation. Water depth explained the most variation (28 %) followed by TP (16 %), magnesium (14 %) and bicarbonate (9 %). These variable names are in bold type on the ordination biplots (Fig. IV-3 & IV-4), and in the table of the final CCA results (Table IV-4). The remaining 6 variables did not explain a significant proportion of the species variation.

For each CCA axis, a linear regression equation (with canonical coefficients for each variable) is computed. These coefficients and the significance of them were determined, and are presented as canonical coefficients and t-values (Table IV-4). Water depth and TP concentration contributed significantly to axis 1, while depth, lake area, calcium, magnesium, bicarbonate and TP concentration contributed significantly ($p \leq 0.05$) to axis 2 (Table IV-4). Depth and TP concentration increased from left to right on axis 1 (Fig. IV-3 & 4). All variables except for TP concentration increased from bottom to top on axis 2. TP concentration increased from top to bottom on axis 2. The intra-set correlation coefficient represents the correlation between the environmental variable and the axis (ter Braak, 1987). The highest intra-set correlation on axis 1 was for water depth (Table IV-4). Magnesium, bicarbonate and chloride had the highest intra-set correlations on axis 2. Only magnesium and bicarbonate were (as identified through forward selection) significantly related to diatom species distributions.

Samples showed good separation along axes 1 and 2 (Fig. IV-3). Species also showed separation along both axes, although the range in scores was lower than for the samples (Fig. IV-4). Only species with more than two occurrences in the data set were plotted (Fig. IV-4 & IV-5). Symbols indicate the number of times a species occurred in the data set of 80 lakes. Species numbers with corresponding names, actual and effective number of occurrence (N2), and maximum relative abundance are given in Table IV-5. Presence of species in lakes from different geographical regions is indicated.

It was determined through forward selection, significant canonical coefficients, and intra-set correlations that water depth was the most important variable in the data set. On the ordination diagram, lakes deeper than 3.5 m (indicated by solid circles) generally separated from the shallow lakes, although there were some exceptions (Fig. IV-3). Variables other than water depth influenced the deeper lakes located on the left side of the ordination diagram. The shallow and deep lakes were located throughout all ecoregions of the province.

In this data set, many lakes had a maximum water depth less than 3.5 m (Table IV-2). Most of these were clustered on the left side of the first axis (Fig. IV-3). There was little variation between the scores for the shallow lakes on axis 1. All of these samples came from shallow lakes located in northern Alberta. Lakes with water depth greater than or equal to 3.5 m were generally on the right side of the axis. These samples came from deep lakes located in central and northern Alberta. There was much variation between the scores for these samples. One lake from western Alberta (number 61) and one from eastern Alberta (number 71) had similar ordination scores along both axes 1 and 2.

Samples in the lower right corner of the biplot included 7 deeper lakes from the Boreal Forest region of northeast Alberta (samples 5 – 10, 21 & 28), 1 lake from the

Montane Boreal Forest (61), and 1 lake from the Boreal Forest– Parkland transition ecoregion (71). *Asterionella formosa* (17), *Aulacoseira ambigua* (19), *Cyclotella radiosa* (34), and *Stephanodiscus parvus* (153) occurred in these lakes. These lakes positioned in the lower corner do not have unique species assemblages since the species had cosmopolitan distributions in Alberta (Table IV-5).

Lakes from the southern most Boreal Forest region (samples 70, 76, 77, 79, 80, 83 & 84) were positioned across axes 1 and 2 in the upper right corner of the biplot (Fig. IV-3). Benthic *Fragilaria* species dominated in sample 83 (86 %), while small *Cyclotella* species dominated in sample 77 (51 %). In samples 79 and 80, benthic *Fragilaria* species were dominant (65 & 40 %, respectively), while 2 planktonic species, *Aulacoseira granulata* (21) (15 & 16 %, respectively) and *F. crotonensis* (77) (11 & 7 %), respectively were sub-dominant species in the assemblages. In samples 76 and 84, *A. granulata* was a dominant species (46 & 28 %, respectively), while *Stephanodiscus parvus* (153) was a sub-dominant species (15 & 10 %, respectively) in the assemblages. In the final sample (70) from this ordination group, *A. ambigua* (19) and *F. crotonensis* were co-dominants (19 % each) in the diatom assemblage. These lakes are geographically close, but had different diatom species assemblages.

A gradient in dissolved ions and nutrients separated the deep lakes along the right side of axis 2. Lakes at the bottom of the axis (e.g., samples 6, 7, 8, 9, & 10) generally had lower bicarbonate and magnesium, and higher TP concentration than the lakes towards the top of the axis (e.g., samples 75, 77, 79, 80, & 81). The former lakes had assemblages of species including *Asterionella formosa* (17), *Aulacoseira ambigua* (19) and *Stephanodiscus parvus* (153), while the latter lakes had assemblages of species including *Aulacoseira granulata* (21), *Cyclotella distinguenda* (30), *C. pseudostelligera* (33), and *Fragilaria crotonensis* (77).

Most of the shallow lakes were positioned on the left side of the first axis, and dispersed across the second axis. Magnesium and bicarbonate were important variables on this axis, and the lakes were distributed along concentration gradients of these 2 variables. These lakes (samples with open circles in Fig. IV-3, 1 – 59, 67 & 68) were variable in nutrients and chemistry (14-185 µg TP/l; 0-229 mg HCO_3/l). Many of these small lakes can be classified as wetlands. For example, lake 48 was large (31.58 km^2), shallow (.9 m) and high in nutrients (410 µg TP/l). The diatom community was mainly benthic (82 %) dominated by small epipelic species of *Fragilaria* (72 %).

Geographically close lakes were not necessarily grouped together on the biplot. Lakes from the Caribou Mountains (samples 35 - 44, 67 & 68), except for sample 40 which will be discussed below, were grouped along axis 1, but were spread out along axis 2 from top (68) to bottom (67). Lakes from the Buffalo Head Hills (samples 45 – 56) were also spread out along axis 2 from top (52) to bottom (55). All of these lakes were shallow, and they had little dispersion on axis 1. Samples at the bottom of axis 2 (e.g., samples 11, 12, 25 & 67) had lower concentrations of magnesium and bicarbonate and higher concentrations of TP than the samples at the top of the axis (e.g., samples 31, 38, 42, 53 & 65). The former group of shallow lakes had assemblages of species including *Achnanthes suchlandtii* (9), *Aulacoseira ambigua*, *A. italica* (22), *F. construens* v. *venter* (76), and *Navicula submuralis* (162). The latter group of shallow lakes had assemblages of diatom species including *Achnanthes linearis* (6), *Navicula laevissima* (115), *N. leptostriata* (117), *N. radiosa* (122), and *Nitzschii fonticola* (133).

Conversely, some geographically close lakes were positioned close together on the ordination biplot. For example, samples 12 & 15, 18 & 26, 23 & 24, 42 & 68, 49 & 51 (in northern Alberta), 84 & 76 (in central Alberta) have similar geographical locations, and they were positioned close together on the ordination biplot. Species assemblages were similar in the above pairs of lakes. *Fragilaria construens* var. *venter* (76) and *F. pinnata* (85) were common species in most of these lakes. Other species were characteristic to individual pairs of lakes. *Achnanthes suchlandtii* (9), *A. subatomoides* (11) and *Navicula radiosa* (122) were common to lakes 18 and 26, while *N. pupula* (121) was common to lakes 23 and 24. *Gomphonema minutum* (96) and *N. cuspidata* (104) occurred in lakes 42 and 68, while *Amphora pediculus* (13), *Cocconeis placentula* (29), *Cyclotella stelligera* (35) and 3 species of *Navicula* occurred in lakes 49 and 51. Finally, *Aulacoseira granulata* (21), *Stephanodiscus niagarae* (152) and *S. parvus* (153) (all planktonic species) were common to the deeper lakes (76 & 84).

Lakes 44 and 45 were included in the final CCA, but were not included on the biplot (Fig. IV-3) because they were extremely different from all other lakes. The ordination scores for these lakes on axis 1 were within the range of all values (-1.12 & -

1.18, respectively), but on axis 2 the scores were extremely high compared to the range of all values (4.22 & 5.81, respectively). Dominant diatom species in these lakes were *Cocconeis placentula* (29)(55%) and *Amphora libyca* (12)(33%), respectively. These species were found in low abundance in all other lakes, 1-11% (in 26 lakes), and 1-8% (in 26 lakes), respectively.

Some lakes did not fit into the simple separation of deep and shallow lakes (Fig. IV-3). Some deeper lakes (≥ 3.5 m) were located among the shallow lakes. Chemistry of these lakes was similar to the chemistry of the shallow lakes in this data set (Table IV-2). Lakes 11, 30, 32, 63 & 66 were deeper lakes (≥ 3.5 m) positioned on the left side of the x-axis. Lake 32 (3.6 m, 9 µg TP/l, 4 % plankton) was positioned in the upper left corner. The diatom assemblage from this lake (located in northeastern Alberta) was dominated by *Navicula laevissima* (115) (46%). This species occurred in 19 other lakes, but always at ≤ 10 % relative abundance in those lakes. This is a clear water lake, with a well-developed epipelic diatom flora. Sample 30 was a moderately sized (4.7 m; 4.4 km^2), mesotrophic (18 µg TP/l), hard water (61.1 mg HCO_3/l) lake, with *Tabellaria flocculosa* strain IIIp (157) (21 %) as the dominant species. Depth was 8 m and phosphorus concentration was 8 µg TP/l in sample 63. The flora was benthic (99 %), dominated by small epipelic *Fragilaria* species (69 %). The diatom flora was very different from other lakes of similar depth (e.g., samples 69, 74 & 77). They had larger planktonic populations (87 %, 91 %, & 52 %, respectively), and higher TP concentrations (Table IV-3). Samples 11 and 66 had very different concentrations of TP, 42 and 10 µg TP/l, respectively, but had equal relative plankton abundance (53 %). *Aulacoseira ambigua* and *A. italica* dominated in sample 11, while *A. distans* (20) and *Cyclotella stelligera* (35) dominated in sample 66.

Lakes 22 and 40 (1.3 m & 2.5 m deep, respectively) were positioned on the right side of axis 1, among the deeper lakes of the data set. Lake 22 was at the low and high ends of bicarbonate and TP concentration, respectively. Measurements indicated this was a small (.91 km^2), high bicarbonate (43 mg/l), and nutrient rich (85 µg TP/l) lake, with both benthic and planktonic species. Dominant species included *Aulacoseira ambigua* (9%), *A. italica* (9%), *F. construens* v. *venter* (33%), *F. pinnata* (85) (10%), and *Stephanodiscus parvus* (15%). Lake 40 (4.77 km^2) was positioned within the grouping of deep lakes even though it was shallow (2.5 m). It had high concentrations of nutrients (125 µg TP/l) and bicarbonate (112 mg/l). Dominant diatom species were *Asterionella formosa* (17) (15%), *Aulacoseira ambigua* (19) (16%), *A. granulata* (21) (29%), and *S. niagarae* (152) (16%).

Most of the species scores in the ordination analysis were between –1.2 to 0.9 on the x-axis, and -0.9 to 0.95 on the y-axis (Fig. IV-4 & IV-5). Typical planktonic species were located on the right side, but some also occurred on the left side of the x-axis. They were mainly positioned along the water depth gradient. Of all the species in the analysis, most were positioned on the left side of the x-axis, and dispersed along the y-axis between -0.9 to 2.0. These were predominantly benthic species. These were the species present in the shallow lakes that were also located on the left side. Species scores from the direct ordination analysis (CCA) are indicated by symbols. These symbols represent the number of times each species occurred in the 80 lake data set. Common benthic species were *Achnanthes lanceolata* (4), *Amphora libyca* (12), *A. pediculus* (13), *Cocconeis placentula* (29), *Fragilaria brevistriata* (69), *F. capucina* (70), *F. construens* var. *construens* (74), *F. construens* v. *venter* (76), *F. leptostauron* v. *martyi* (81), *F. pinnata* (85), *Navicula laevissima* (115), *N. pupula* (121), and *N. radiosa* (122). Common planktonic species were *Asterionella formosa* (17), *Aulacoseira ambigua* (19), *A. italica* (22), *Cyclotella stelligera* (35), *Fragilaria crotonensis* (77), *Stephanodiscus niagarae* (152), *S. parvus* (153), and *Tabellaria flocculosa v. flocculosa* strain IIIp (157). All of these species occurred in more than 20 lakes, but the maximum abundance of these species varied between 5 to 76 % (Table IV-5).

IV.D.3. Species Distributions and Assemblages

Species richness ranged between 4 to 29 species per lake in the 80 lake data set (Fig. IV-6). This is an indication of diatom diversity in Alberta lakes. Average species richness (number of diatom species in a lake) was 14.3. There were more lakes (n=46) with less than the average number of species, than lakes (n=34) with more than the average number of species. High species richness occurred in lakes throughout the province and not only in lakes from one region or another.

The frequency of species occurrences in the 80 lake data set has a positively skewed distribution (Fig. IV-7). Species occurred between 1 to 70 times over 80 lakes. There were many species (65) with 5 or fewer occurrences, and few species (7) with more than 30 occurrences. The remaining species (44) occurred in 6 to 30 lakes. On average each species occurred in 10 lakes. *Fragilaria* species were among the five most common species. The most common species were *F. pinnata* (85), *F. construens* v. *venter* (76), *F. brevistriata* (69), *Aulacoseira ambigua* (19), and *F. construens* v. *construens* (74). They occurred in lakes across the province. Relative percent abundance of these 5 species across 80 lakes is illustrated (Fig. IV-8).

The 5 most common species occurred in at least 39 lakes. Diversity indices (N2) for these 5 species ranged between 15 to 41 (Table IV-5). An N2 value close to the number of occurrences indicates that relative abundance is similar between lakes (Wilson *et al.*, 1996). Rare species tended to have even abundance among lakes. Some common species had even relative abundance (e.g., *Achnanthes linearis* (6), *A. suchlandtii* (9), *Navicula submuralis* (162), and *Nitzschii palea* (136)), while some had uneven relative abundance (e.g., *Cocconeis placentula* (29), *Cyclotella stelligera* (35), *Navicula radiosa* (122), and *Stephanodiscus niagarae* (152)). Of the cosmopolitan species, *F. construens* var. *venter* had the most even abundance in the 80 lakes.

Fragilaria construens v. *construens* occurred in 39 lakes from all parts of the province, but generally not in the deeper lakes. Relative abundance was 1-11% in 35 lakes, and 23-34% in 4 lakes. This species usually only occurred at low relative abundance, but had the highest relative abundance in the remote northern lakes (samples 24, 34, 35 & 63). It was most abundant in shallow lakes, with low concentrations of TP, moderate concentrations of magnesium and high concentrations of bicarbonate.

Aulacoseira ambigua occurred in 41 lakes. Relative abundance was 1-19% in 34 lakes and 26-36% in 7 lakes. This species was not restricted to one geographic region, although it was found more often and at higher abundance in lakes of the boreal region as compared to lakes of the parkland region. This species occurred in lakes with moderate water depth, and higher concentrations of TP and bicarbonate.

F. brevistriata occurred in 50 lakes, with low relative abundance (1-17%) in 44 lakes, and high abundance (22-58%) in 6 lakes. It occurred in lakes from all regions, but at higher relative abundance in the northern boreal lakes.

F. construens v. *venter*, a common epipelic species, occurred in 68 lakes at 1-76% relative abundance. Relative abundance was 50 – 76 % (in 8 lakes), 20 – 49 % (in 28 lakes), and 1 – 19 % (in 32 lakes). This species occurred at high abundance in the northern lakes, and in low to zero abundance in some parkland lakes. It occurred in lakes with shallow water, high concentrations of TP and moderate concentrations of magnesium and bicarbonate.

F. pinnata was the most common species, and occurred in 70 lakes at 1-61% relative abundance. This species occurred at high to very high abundance (20 – 61 %) in 16 lakes, and at low abundance (1 – 19 %) in 54 lakes. *F. pinnata* was very common in lakes of the montane, central boreal and north-central boreal ecoregions, but was less common in the 4 lakes on the Canadian shield. It is a cosmopolitan species that can tolerate a wide range of conditions.

There were 22 diatom species found in lakes from all areas of the province (Table IV-5). Thirteen of these species occurred in more than 10 lakes. Four of the five most common species in the data set were epipelic forms, while only one was a planktonic form. The two most common species (*Fragilaria pinnata* and *F. construens v. venter*) were small, epipelic forms. When *F. construens v. venter* was present in a lake, it generally had a larger relative abundance than *F. pinnata*. The next three most abundant species (*F. brevistriata, Aulacoseira ambigua*, and *F. construens v. construens*) occurred abundantly in only a few lakes. Generally, when they were present they represented a small portion of the diatom assemblages.

Some of the rare species (occurring in ≤ 5 lakes) of the data set occurred in lakes from specific regions of the province (Table IV-5). The maximum relative abundance of these rare species in any 1 lake ranged between 1 to 46 %. *Aulacoseira lirata* (23), *Caloneis bacillum* (25), *Navicula jaernefeltii* (111), *Pinnularia gibba* (141) and *Tetracyclus lacustris* (158) were only found in the lakes from the Birch Mountain area. *Epithemia argus* (51), *Eunotia bilunaris* (56), *Gomphonema angustum* (91) and *N. digitulus* (107) were only found in lakes from the Caribou Mountains. *Diploneis* *occulata* (46) occurred only in the lakes in the extreme west (samples 58, 62 & 88) and *Eunotia* species had low relative abundance in any lake, but also only occurred in lakes from the Birch and Caribou Mountains (zones I & II in Table IV-5). Many other rare species were found in lakes from two areas of Alberta. *Achnanthes peragalli* (8), *Aulocoseira distans* (20), *Cocconeis disculus* (27), *Cyclotella tripartita* (36), *Frustulia rhomboides* (89), *Gomphonema gracile* (94), *Navicula minima* (114), *N. pseudoventralis* (120), *N. recens* (123), *Neidium affine* (127) and *Nitzschii heufleuriana* (134) were some of these species. Species such as *Cyclotella håkanssoniae* (31), *Cymbella cesatii* (39), *Fragilaria capucina* var. *mesolepta* (71), *Navicula harderii* (110), *N. seminulum* (125) and *Nitzschii linearis* (135) were found in lakes from three areas in Alberta. Only two rare species, *Cocconeis neodiminuta* (28) and *F. parasitica* (84), were found in lakes from four different geographical areas.

Some widely distributed species, e.g., *Nitzschii amphibia* (132) and *Tabellaria flocculosa v. flocculosa* str. *III* (157) were more common to, but not restricted to, lakes of the north. Conversely, *Fragilaria crotonensis* (77) was more common to, but not restricted to, lakes of the central region.

From the 80 lakes, 20 planktonic species from the genera *Asterionella, Aulacoseira, Cyclotella, Fragilaria, Stephanodiscus,* and *Tabellaria* were identified. There were 1-41 occurrences of species from these genera. Some species, e.g., *Asterionella formosa* (17), *Fragilaria crotonensis* (77), and *Stephanodiscus parvus* (153), had similar abundances between lakes, while other species, e.g., *Aulocoseira granulata* (21), *Cyclotella distinguenda* (30), *Fragilaria nanana* (82), and *Stephanodiscus niagarae* (152), varied in relative abundance between lakes (Table IV-5). These species occurred in lakes from all geographic regions.

Relative percent abundance of benthic and planktonic assemblages varied with lake water depth (Fig. IV-9). Generally, planktonic assemblages were more important in the deeper lakes, and benthic assemblages were more important in the shallower lakes. Extreme exceptions included samples 67 (.9 m, 58 % plankton), 40 (2.5 m, 84 % plankton), 10 (3.5 m, 73 % plankton) 88 (3.5 m, 7 % plankton), 32 (3.6 m, 4 % plankton), 63 (8 m, 1 % plankton), and 83 (8 m, 4 % plankton). Lakes 67 and 40 were shallow (< 3m) but had concentrations of TP that were in excess of 70 µg/l. Lake 10 was moderately deep, with a very high concentration of TP (210 μg/l), low concentration of magnesium (4 mg/l) and moderate concentration of bicarbonate (41.1 mg/l). Lakes 32, 63 and 83 had water depth more than 3.5 m, but the former 2 had low concentrations of TP(9 & 8 μg TP/l, respectively), while the latter had a higher concentration of TP (49μg/l). Lake 88 was an exception. It was 3.5 m deep, and had a very high concentrations of TP (209μg/l), magnesium (38.3 mg/l), and bicarbonate (201.3 mg/l).

IV.E. Discussion

IV.E.1. Data Screening

The original data set consisted of lakes found across a wide range of biological and climatological conditions (Fig. IV-1 & IV-2; Table IV-1). The difference in chemistry between these lakes was immediately apparent (Table IV-2 & IV-3). Lakes in northern Alberta were small and shallow, while lakes in central Alberta were larger and deeper. Depth played an important part in this data set and it appeared to be an overriding factor to diatom species composition as compared to geography, climate or dominant catchment vegetation.

Three outlier samples (14, 54 & 82) were detected by using DCA on the species data. These 3 lakes were quite different from all other lakes in the data set. They each had unique features that made them outliers. In this data set they were significantly different, but in comparison to all lakes they may not be that unusual (Hall & Smol, 1992). After removal of these outlier samples indirect ordination analysis (CA) revealed good separation of samples and species along the first 2 axes. This indicated that there was underlying variation in the species data. By using direct ordination (CCA) methods, some of this variation may be accounted for by measured environmental variables (ter Braak, 1987).

The data screening procedure was applied to 87 lakes and 14 environmental variables. Four environmental variables and 7 lake samples were removed through these procedures. These 7 samples had slightly unusual environmental variables. The values for the variables were not extremely different, but there was a large range between the value for one lake and the next recorded value. For example, sample 85 was extremely deep (60 m) compared to the next closest sample (number 71, 28 m). The removal of sample 85 decreased the range of lake water depth, but more importantly it revealed other important environmental gradients within the remaining lakes of the data set. The presence of these extreme samples skewed the distribution of samples across the environmental gradients. The removal of them revealed the separation of the samples along shorter environmental gradients.

IV.E.2. Ordination

A CCA performed on the final data set of 80 lakes produced high and significant eigenvalues. These were slightly lower than eigenvalues computed from the indirect ordination. Lower eigenvalues occur with CCA as compared to CA because in the former method site scores are restricted by environmental variables and the axes are linear combinations of environmental variables (ter Braak, 1987). The eigenvalue computed for each axis represents maximum dispersion of species scores (ter Braak, 1987). Analysis of the species data by indirect ordination (CA) produced a similar grouping of the samples. Low cumulative percent variance in the diatom data was explained by the first 2 axes, but this is expected in large data sets with many zero values (Stevenson *et al.*, 1991). The results obtained from this final ordination were comparable to other studies (Dixit *et al.*, 1991; Hall & Smol, 1992; Christie & Smol, 1993; Jones *et al.*, 1993; Pienitz & Smol, 1993; Bennion, 1994; Reavie *et al.*, 1995) for eigenvalues and percent variance explained by diatoms and diatom-environment relationships. Correlations between the species and environmental variables on the first 2 axes (R_1 & R_2) from this study were also comparable to other studies (Agbeti, 1992; Hall & Smol, 1992; Bennion, 1994; Reavie *et al.*, 1995).

Important and significant variables in the data sets are determined through forward selection, canonical coefficients and intra-set correlations (ter Braak, 1987). In some cases interpretation of relationships is best done through the use of intra-set correlation values over canonical coefficients due to the occasional instability of some coefficients (ter Braak, 1986). Water depth was the most influential variable affecting diatom species distribution (Table IV-4; Fig. IV-3 & IV-4). In the ordination diagram, deep lakes were positioned on the right side of axis 1 (Fig. IV-3). These samples were separated along a depth gradient on axis 1 and along gradients of bicarbonate, magnesium and TP on axis 2. Water depth has also been identified as a significant variable in other studies (e.g., Hall & Smol, 1992; Christie & Smol, 1993; Fritz *et al.*, 1993; Reavie *et al.*, 1995). As water depth increases, the area of substratum within the photic zone available for colonization decreases, while the volume of water available for buoyant and/or motile forms increases. A larger planktonic population increases shading of the sediment, decreases light availability, and can lead to changes in species assemblages. Water depth can thus influence the species and communities that dominate in a lake.

In this data set the importance of water depth was likely due to the wide range in values (Table IV-3). This extreme range (27.5m) emphasizes the dispersion of lakes with minimum and maximum lake depth. Water depth is always an important variable due to its influence upon community structure, but its importance decreases as depth range decreases (Fritz *et al.*, 1993), or as the range in other variables, such as TP concentration, increases (Reavie *et al.*, 1995). The significance of water depth on diatoms has been shown by the development of a significant equation between diatoms and water depth (Yang & Duthie, 1995).

Planktonic species are more sensitive to changes in water chemistry (Wetzel, 1975; Turpin, 1988). Studies that focus on deeper lakes will have larger planktonic assemblages. These lakes have assemblages of species that are influenced in a similar manner. In addition, nutrients utilized by planktonic algae come directly from the water column, and variations in nutrient concentrations over the seasons result in planktonic species succession (e.g., Round & Brooks, 1959; Hickman, 1979; Anderson, 1995; Moss *et al.*, 1997). A strong relationship between planktonic species and water chemistry variables is thus expected (Zhang & Prepas, 1996).

Shallow (0.5 – 3.0 m) and small (0.21 - 6.5 km^2) lakes dot much of northern Alberta. These small lakes are located within the Boreal Forest ecoregion (Fig. IV-1), an area with abundant peatlands (Vitt, 1992; Vitt *et al.*, 1994). Chemistry was variable within the shallow lakes from northern Alberta. These lakes were dispersed along gradients of dissolved magnesium, bicarbonate and TP concentration. Variations in planktonic abundance (0 – 58 %) in these lakes was possibly due to variations in dissolved TP (Schindler, 1985).

Lakes 44 and 45 (northern Alberta) both had large populations of two species, *Cocconeis placentula* (29) and *Amphora libyca* (12), respectively, that were otherwise rare in any other lake. *C. placentula* is an epiphytic, alkaline tolerant, cosmopolitan species (Lowe, 1974; Beaver, 1981; Hickman, 1982). It represents up to 90% of epiphytic algae on some macrophytes (Reavie & Smol, 1997), it has a high total nitrogen optimum (Christie & Smol, 1993), and is otherwise rare in most data sets (Agbeti, 1992; Cumming & Smol, 1993; Wilson *et al.*, 1996). It dominated in a small, shallow pond, with abundant nutrients and moderate bicarbonate and magnesium concentrations (Table IV-2). This species is indicative of the presence of macrophytes and productive, hard waters.

Amphora libyca is an epipelic, perhaps alkaline tolerant species (Lowe, 1974; Beaver, 1981) found on organic and calcareous sediments in mesotrophic to eutropic lakes (M. Hickman, personal communication). This species has not been recorded in many studies, but did occur up to 91% relative abundance in a lake from British Columbia (Wilson *et al.*, 1996). Little information has been published about this species, presumably because it is usually only present at low relative abundance. Based on the presence of *A. libyca* in Alberta lakes, it is inferred that this species prefers shallow water with high concentrations of phosphorus and alkaline ions, but more information needs to be gathered on this relationship.

Most of the deep lakes (≥ 3.5 m) were positioned on the right side, while the shallow lakes (< 3.5 m) were positioned on the left side of the ordination diagram (Fig. IV-3). Samples 11, 30, 32, 63 and 66 (all > 3.5 m)were positioned on the left side. Low concentrations of phosphorus and some ions limited phytoplankton communities in some of the lakes, and the dominance of different species in other lakes.

Navicula laevissima (an epipelic species) dominated in the lake 32. Very low concentrations of TP, plus low concentrations of magnesium, sodium, calcium, nitrogen, organic carbon, but high concentrations of silica, seem to have limited phytoplankton. This provided a clear water column and the opportunity for a large benthic population to develop. Interestingly, in this data set, *N. laevissima* only occurred in lakes north of 54° N, and of all the lakes in which it occurred, only 2 of those lakes had maximum water depth greater than 3.5 m. It is inferred that *N. laevissima* is an indicator of ultra-oligotrophic, clear water lakes.

Lakes 63, 66, 30 & 11 were positioned along axis 2 along an increasing gradient of TP concentration. The dominant species present in these lakes also reflected this gradient. *Fragilaria* species dominated in sample 63, since low dissolved phosphorous limited phytoplankton populations. Epipelic species develop best when there are few phytoplankton cells that may block incoming radiation (Hansson, 1988), and *Fragilaria* species are also typical of a clear water lake. The dominant species found in sample 66 (*Aulacoseira distans* and *Cyclotella stelligera*) are oligotrophic indicators. In sample 30 (*Tabellaria flocculosa* strain IIIp) the dominant species is a mesotrophic indicator, while in sample 11 the dominant species, *A. ambigua* and *A. italica*, are eutrophic indicators (Agbeti & Dickman, 1989; Fritz *et al.*, 1993; Bennion, 1994; Reavie *et al.*, 1995). The species assemblages in these 4 lakes may reflect the TP concentration gradient, but the relative size of the planktonic community (1%, 53%, 29% and 53%, respectively) did not reflect the increasing gradient. Increased nutrients do not necessarily result in an increase of phytoplankton. Other factors such as lake water volume, and water retention time can affect the availability of nutrients.

In contrast, some shallow lakes (< 3.5 m depth) were positioned on the right side of the ordination diagram. The presence of the planktonic species made samples 22 and 40 similar to the deeper lakes that also had dominant planktonic communities. These 2 lakes are hyper eutrophic in comparison to the previous group of lakes (11, 30, 63 & 66). It appears that chemistry of the water (abundant nutrients) influenced the diatom assemblage, leading to a large planktonic community, shading of the sediments and a reduced benthic community.

Some geographically close lakes were also close on the ordination biplot. It has been observed that lakes may or may not cluster together in ordination analyses according to geography (e.g., Christie & Smol, 1993; Pienitz & Smol, 1993; Bennion, 1994; Reavie *et al.*, 1995). Most of the shallow lakes of the Birch Mountains (Northeastern Alberta) clustered in the lower left corner. These lakes on the left side of the ordination all had low water depth and low concentration of magnesium, but overall variable relative percent plankton, TP and bicarbonate concentration values. Differences in catchment size, and slope in the catchment affect the rate of nutrient input into a lake basin (Hall & Smol, 1993). Lakes from one area may have similar influences from the respective catchments due to similar vegetation in geographically adjacent lakes. Similar influences upon lakes are reflected in similar scores in ordination analyses.

Lakes from the Caribou Mountains (northern Alberta) were scattered along the left side of the y-axis. Underlying factors such as lake and catchment size, catchment slope (which affects rate of water and nutrient input), lake water retention time, number of inflows and outflows (and flow rates), and type and extent of anthropogenic development in the catchment may account for variations in the lakes (Hall & Smol, 1993). These are all underlying factors that were not accounted for in the environmental data. Inclusion of them may help to explain more of the variation in the species data since these factors can influence water chemistry, and thus species composition. These factors may determine which lakes are likely to be most similar.

IV. E. 3. Species Distributions and Assemblages

Species richness varied between lakes (Fig. IV-6). These numbers have not been reported for other similar studies, so it is not known if these are low or average. Ocean planktonic diatoms generally develop largest populations in colder water, but even if species number is high, the total number of organisms is low (Round, 1981; Lee, 1989). In addition, growth of diatom populations is directly related to silica concentration in the water. The number of diatom species can be related to silica availability, or availability of other nutrients (Lee, 1989). This variable was incomplete for this data set so relationships between silica concentration and species diversity cannot be considered at this time. It was determined that an inverse relationship between number of diatom species and TP concentration was significant (r=0.4) (results not shown). This relationship was likely only significant due to the large sample size. Bradbury and Waddington (1973) concluded that decreased number of species over time was due to cultural eutrophication. This initially suggests that few diatom species can tolerate hyper-eutrophic conditions, and that species will be lost in culturally eutrophic lakes. Including all algal species, and changes in total species richness across a TP concentration gradient could extend these analyses further. Recent fossil assemblages of diatoms from lakes could be analyzed (using palaeolimnological methods) to determine if diatom species richness has changed over settlement history.

Effective number of species occurrences in the data set was determined by N2 values (Table IV-5). An N2 value close to the total number of occurrences in all lakes indicates that species relative abundance is similar between lakes of the data set (Wilson *et al.,* 1996). Effective (N2) and actual (number of lakes in which present) occurrences varied greatly among species (Table IV-5). N2 has also been used as a measure of diversity (Reavie & Smol, 1997). An N2 value close to 1 indicates that a species is very abundant in one sample, while rare in all other samples (Wilson *et al.,* 1996; Reavie & Smol, 1997). Thus, N2 value for species is affected by abundance in multiple lakes. Many species in this data set and in other data sets (Wilson *et al.,* 1996; Reavie & Smol, 1997) had unequal abundance between lakes. In data sets with many species, or even in smaller data sets, unequal species abundance can be expected. If optimal conditions for a particular species are present in a lake, then that species will typically be found in highest abundance in that lake (ter Braak & van Dam, 1989).

The distribution of the number of occurrences for each species in the data set is positively skewed (Fig. IV-7). There were many rare species (65), few common species (7), and some species (44) with intermediate levels of occurrences. This suggested that many of these lakes had unique combinations of diatom communities, and unique dominant and sub-dominant species. This same distribution has also been observed for the number of individuals per species in one sample (Barbour *et al.,* 1987). On a log-normal scale, the distribution has a bell shaped curve. As sample size increases, and the focus is shifted to number of species occurrences in all samples, this same distribution can be expected. In other cases a small sample (e.g., diatom valves counted in a sample) may not show this bell-shaped distribution of individuals (Barbour *et al.,* 1987). The same would hold true for number of samples. As the sample number decreases, the probability of missing some rare species increases.

Species were grouped according to predominant geographical location (Table IV-5). Half of the species were restricted to the small and shallow northern Alberta lakes (Table IV-5, areas I, II & III), and most of them were benthic, mainly epipelic or epiphytic. Central Alberta has many recreational lakes, and many of the species were mesotrophic to eutrophic planktonic indicator species (i.e. *Aulacoseira granulata, Fragilaria crotonensis,* and *Stephanodiscus niagarae*) (Fritz *et al.*, 1993; Reavie *et al.*, 1995). In comparison to most of the lakes from northern Alberta, these lakes from central Alberta were typically deeper, and due to continuous impacts (agriculture, cottage development, etc.) they generally had higher dissolved nutrients (Table IV-3; Fig. IV-3).

It was expected that a shallow lake would have a larger benthic community, while a deep lake would have a larger planktonic community. This did not always occur in all lakes of this data set (Fig. IV-9). Extreme exceptions ranged from a shallow lake (.9 m) with 58 % planktonic individuals (sample 67), to a deep lake (8 m) with 96 % benthic individuals (sample 83). These shallow lakes, or wetlands, had high planktonic populations when TP concentration was also high. This was also found in some eutrophic ponds in England (Bennion, 1994). Conversely, lakes with deeper water, but very low concentrations of TP, had very low plankton populations. Phytoplankton populations are limited by availability of nutrients (Schindler, 1985). Total phytoplankton biomass is also positively related to TP concentrations (Zhang & Prepas, 1996). In general, the planktonic species responded to variations in the chemical composition of the water.

In comparison to other areas regions, most of the lakes in this data set are eutrophic (50 µg TP/l) (Forsberg & Ryding, 1980). Some of these Alberta lakes also had very high concentrations of bicarbonate, alkalinity (mg $CaCO_3$/L), magnesium and calcium. These values were on average higher than values recorded for alkalinity in Southeastern Ontario (Christie & Smol, 1993) and Michigan lakes (Fritz *et al.*, 1993). These lakes also had higher conductivity, conductivity and calcium, and conductivity, calcium, and magnesium than lakes in British Columbia (Reavie *et al.*, 1995), in the Northwest Territories (Pienitz & Smol, 1993), and in Antarctica (Jones *et al.*, 1993), respectively.

Sample 88 had very high concentrations of TP (209 µg/l), magnesium (38.3 mg/l), and bicarbonate (201.3 mg/l), while only 7 % of the diatom valves were planktonic species. There are many factors that can affect plankton population size (Round, 1981). Available dissolved nutrients are one such factor. Some of these lakes had high bicarbonate, magnesium, and TP concentration. It appears that even when nutrients are abundant that high water hardness, caused by high concentrations of calcium, magnesium and bicarbonate (Wetzel, 1975), can influence plankton population size. In saline lakes, when conductivity increases, chlorophyll *a* concentration (a proxy for phytoplankton blooms) decreases (Evans & Prepas, 1996). They observed that an increase in conductivity, due to the concentration of saline ions, decreased or suppressed algal productivity. It is suggested that high concentrations of alkaline earth metals, as found in very hard water lakes (Wetzel, 1975), will also cause a suppression of algal productivity. Lake 88 was an extreme example of this suggested link. Some other lakes (e.g., 75, 79, 83 & 87) had relatively low plankton populations in the presence of moderate to high concentrations of TP. The bathymetry of this lake has not been mapped, but average Secchi depth measurements are between 2.3 to 3.4 m (Mitchell & Prepas, 1990). It is possible that a benthic community developed due to sufficient illumination of the sediments. This situation is in contrast to other lakes with very high TP concentration and dominant planktonic assemblages. Perhaps high water hardness is only a limit to diatom phytoplankton populations. It has been observed that cyanobacteria form large populations in some of the central Alberta lakes (Evans & Prepas, 1996; Zhang & Prepas, 1996). Populations of cyanobacteria were not measured in this study, but based on other studies done in Alberta, they likely formed large populations in some of these lakes. Cyanobacteria are good competitors when there are high ratios of phosphorus to other nutrients and when nitrogen is limiting. The possible relationship between algal assemblages and water hardness should be investigated further.

IV.F. Conclusions

The sedimentary diatom assemblages from 93 Alberta lakes were analyzed. The influence of the lake chemical and physical variables on the distribution of diatom species was statistically determined. Depth of the lake water was the most important variable. In large part it determined the predominant diatom community in a lake. Water chemistry variables such as concentration of TP, magnesium and bicarbonate also significantly influenced species distributions. The diatom species responded to variations in these variables.

In the original data set of 93 lakes, 51 were shallow. Many of these should be referred to as wetlands due to their shallow depth and generally small area. Even in these small water bodies there was variation in the water chemistry. Gradients in the concentrations of TP, magnesium and bicarbonate were evident. In some geographically close lakes with similar depth, area, and concentration of ions there were great differences in species composition. Variations in the lake catchment can and does influence species assemblages (e.g., Hall & Smol, 1993). These variations in the catchment, such as size, average slope, and inflowing streams, were not accounted for in this study, but they likely would explain some of the underlying variation in the species data.

Most of the lakes from central Alberta were deep. These lakes were distinguished from most of the lakes in northern Alberta by lake water depth, and concentrations of TP, magnesium and bicarbonate. The lakes of the central region of the province were typically higher in dissolved alkaline ions than the lakes from northern Alberta. Many of the lakes from central Alberta also had high concentration of TP. In comparison to other geographical regions, most of these lakes would be classified as eutrophic systems, even though diatom species composition varied across these Alberta lakes. Since many of the central Alberta lakes were deep, they had larger planktonic diatom populations than the lakes from the north. In these lakes there was variation in the planktonic species composition.

There were 209 diatom species identified from these lakes. This number was reduced down to 116 in the final 80 lake data set after data screening procedures. Both benthic and planktonic species were identified. There were many benthic species found in the small lakes from northern Alberta. Many of the benthic species were only found in these small lakes, and many of these species had few occurrences. Some of these species from the small northern lakes were *Achnanthes subatomoides, Fragilaria virescens, Navicula cf. mediocris,* and *Tetracyclus lacustris*. There were also species restricted to the lakes from northern and western Alberta. Some of these species were *Achnanthes linearis, Cymbella ventricosa, Navicula leptostriata,* and *Tabellaria flocculosa* strain IV *sensu* Koppen. The most common species in this data set were small epipelic *Fragilaria* species, and included *F. brevistriata, F. construens* var. *construens, F. construens* var.

venter, and *F. pinnata*. *Aulacoseira ambigua* was the most abundant planktonic species, followed by *Stephanodiscus niagarae, S. parvus,* and then *Asterionella formosa*. All of the *Fragilaria* species and the former planktonic species had cosmopolitan distributions.

The frequency distribution of number of occurrences of each species in the 80 lake data set was a reverse J-shaped distribution curve (Barbour *et al.*, 1987). There were many rare species, few common species, and some species with intermediate number of occurrences. This distribution occurs for the relative abundance of each species in one sample (Barbour *et al.*, 1987), and in this study for the number of occurrences of each species across many samples.

Many of the central Alberta lakes had high concentrations of hard water ions. It was observed that planktonic populations were not necessarily large in lakes with high TP concentration. It was suggested that high water hardness suppressed algal production in the same way that high salinity has been known to suppress algal production (e.g., Evans & Prepas, 1996).

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Table IV-1. Summary of climate data from 6 stations in Alberta (Atmospheric Environment Service, 1993). Location of stations indicated on Fig. IV-1.

Station	Latitude (°N)	Longitude (°W)	Annual Mean Temperature (°C)	Total Precipitation (mm)	No. Days Maximum Temperature >0 °C	Total July Precipitation (mm)	Daily Mean July Temperature (°C)
(A) Red Deer	52° 11'	113° 54'	2.3	470.2	274	87.9	15.8
(B) Edmonton	53° 18'	113° 35'	2.1	465.8	269	101.0	16.0
(C) Ft. McMurray	56° 39'	111° 13'	0.2	464.7	245	79.1	16.6
(D) Grand Prairie	55° 11'	118° 53'	1.6	450.2	266	67.9	16.0
(E) Buffalo	57° 57'	116° 13'				106.8	14.4
(F) Whitesand	59° 26'	114° 54'				70.3	12.5

Table IV-2. List of the 93 lakes used in this study with geographical position and values for selected lake chemical and physical variables. (* indicates omitted from final ordination).

Lake Number	Lake Name	Latitude (°N)	Longitude (°W)	Depth (m)	Area (km^2)	TP (μg/l)	Mg (mg/l)	HCO3 (mg/l)	Legend
1	L4	$57^0 08^1$	$110^0 50^0$	1.30	0.61	40.00	0.50	12.69	
2	L7	$57^0 05^1$	$110^0 45^0$	1.60	0.33	25.00	2.00	15.98	
3	L16	$57^0 02^1$	$112^0 56^0$	2.00	2.21	73.00	9.00	83.00	
4	L17	$57^0 11^1$	$113^0 34^0$	2.00	1.52	25.00	2.50	28.61	
5	L18	$57^0 26^1$	$112^0 37^0$	27.00	43.39	18.00	1.50	23.02	
6	L19	$57^0 30^1$	$112^0 30^0$	10.50	7.25	36.00	4.00	65.00	
7	L20	$57^0 32^1$	$112^0 29^0$	12.50	17.48	33.00	4.00	64.07	
8	L21	$57^0 36^1$	$112^0 36^0$	13.00	17.17	65.00	3.50	54.12	
9	L22	$57^0 42^1$	$112^0 22^0$	16.00	14.58	28.00	4.00	63.14	
10	L24	$57^0 47^1$	$112^0 08^0$	3.50	8.40	210.00	4.00	41.05	
11	L25	$57^0 24^1$	$112^0 56^0$	9.40	16.76	42.00	0.50	12.44	
12	L27	$57^0 35^1$	$113^0 18^0$	2.80	1.25	120.00	0.50	6.84	
13	L28	$57^0 51^1$	$112^0 58^0$	1.80	1.30	80.00	0.50	0.00	*
14	L29	$58^0 03^1$	$112^0 16^0$	1.10	0.65	45.00	0.50	0.00	*
15	L31	$58^0 03^1$	$112^0 14^0$	1.60	0.41	60.00	0.50	3.00	
16	L46	$57^0 46^1$	$112^0 23^0$	1.30	1.20	160.00	1.50	8.39	
17	L48	$57^0 42^1$	$112^0 12^0$	1.10	1.99	98.00	4.00	70.76	
18	L49	$57^0 45^1$	$112^0 35^0$	1.10	2.61	145.00	2.00	9.52	
19	L50	$57^0 40^1$	$112^0 50^0$	0.60	1.61	105.00	4.00	31.72	
20	L51	$57^0 10^1$	$112^0 40^0$	2.60	3.29	65.00	5.00	65.00	
21	L55	$57^0 13^1$	$113^0 02^0$	5.80	2.65	53.00	6.00	93.94	
22	L56	$57^0 12^1$	$113^0 03^0$	1.30	0.91	85.00	3.00	42.70	
23	L57	$57^0 25^1$	$113^0 14^0$	1.40	1.61	50.00	5.00	70.76	
24	L58	$57^0 27^1$	$113^0 05^0$	1.80	1.64	37.00	4.00	48.00	
25	L59	$57^0 35^1$	$112^0 45^0$	1.60	5.04	90.00	2.00	22.20	
26	L60	$57^0 39^1$	$112^0 36^0$	3.00	0.91	140.00	2.00	24.00	
27	L61	$57^0 39^1$	$112^0 35^0$	1.10	1.68	125.00	2.00	25.25	
28	L62	$57^0 33^1$	$112^0 17^0$	6.00	1.48	83.00	8.00	125.00	
29	L63	$57^0 28^1$	$112^0 20^0$	1.10	1.52	113.00	6.00	84.18	
30	L64	$58^0 08^1$	$110^0 47^0$	4.70	4.40	18.00	3.00	61.12	
31	L66	$58^0 07^1$	$110^0 20^0$	2.50	6.50	15.00	2.00	30.62	
32	L67	$58^0 03^1$	$110^0 23^0$	3.60	1.07	9.00	3.00	40.99	
33	L68	$57^0 50^1$	$112^0 28^0$	0.80	0.21	185.00	1.00	13.91	
34	L69	$57^0 52^1$	$112^0 22^0$	0.80	0.36	120.00	6.00	132.98	
35	L70	$59^0 57^1$	$115^0 17^0$	1.10	0.39	23.00	2.00	46.36	
36	L71	$59^0 58^1$	$115^0 15^0$	1.20	0.81	24.00	2.00	58.56	
37	L72	$59^0 49^1$	$115^0 51^0$	0.70	0.48	31.00	2.00	65.76	
38	L73	$59^0 48^1$	$115^0 36^0$	1.40	0.38	21.00	4.00	71.98	

Table IV-2. Continued.

39	L74	$59^{0} 45^{1}$	$115^{0} 38^{0}$	0.80	0.24	78.00	2.00	22.81	
40	L76	$59^{0} 57^{1}$	$116^{0} 32^{0}$	2.50	4.77	125.00	12.00	112.24	
41	L77	$59^{0} 55^{1}$	$116^{0} 37^{0}$	0.80	1.47	125.00	12.00	98.82	
42	L79	$59^{0} 43^{1}$	$116^{0} 22^{0}$	0.70	0.57	30.00	5.00	85.40	
43	L81	$59^{0} 40^{1}$	$116^{0} 45^{0}$	2.00	0.51	70.00	11.00	141.52	
44	L83	$59^{0} 22^{1}$	$116^{0} 54^{0}$	1.20	1.18	58.00	11.00	112.24	
45	L84	$59^{0} 12^{1}$	$116^{0} 25^{0}$	2.30	1.68	68.00	158.00	223.00	
46	L85	$57^{0} 45^{1}$	$116^{0} 15^{0}$	1.10	1.50	130.00	4.00	45.14	
47	L86	$57^{0} 30^{1}$	$116^{0} 15^{0}$	1.10	0.46	68.00	6.00	62.22	*
48	L87	$57^{0} 15^{1}$	$116^{0} 15^{0}$	0.90	31.58	410.00	9.00	138.00	
49	L90	$57^{0} 01^{1}$	$116^{0} 45^{0}$	1.40	1.53	62.00	4.00	68.32	
50	L91	$56^{0} 45^{1}$	$116^{0} 30^{0}$	1.00	1.08	75.00	6.00	118.34	
51	L92	$56^{0} 45^{1}$	$117^{0} 00^{0}$	1.00	0.54	85.00	18.00	155.00	
52	L93	$57^{0} 30^{1}$	$117^{0} 15^{0}$	1.00	2.62	130.00	21.00	229.00	
53	L94	$57^{0} 30^{1}$	$117^{0} 30^{0}$	1.10	0.50	40.00	4.00	69.00	
54	L96	$58^{0} 13^{1}$	$116^{0} 49^{0}$	2.20	2.34	14.00	44.00	226.00	*
55	L97	$57^{0} 45^{1}$	$117^{0} 45^{0}$	2.10	0.61	55.00	1.00	19.40	
56	L98	$57^{0} 45^{1}$	$118^{0} 01^{0}$	1.20	0.73	25.00	0.50	2.32	*
57	L100	$57^{0} 15^{1}$	$119^{0} 40^{0}$	1.50	0.66	68.00	4.00	75.00	
58	L101	$57^{0} 05^{1}$	$119^{0} 45^{0}$	1.50	0.34	100.00	5.00	71.00	
59	L102	$57^{0} 07^{1}$	$119^{0} 53^{0}$	1.10	0.49	85.00	3.00	69.54	
60	L103	$54^{0} 45^{1}$	$119^{0} 45^{0}$	1.00	0.48	28.00	10.00	116.00	
61	L104	$54^{0} 15^{1}$	$119^{0} 45^{0}$	11.00	0.54	12.00	10.00	138.00	
62	L105	$54^{0} 30^{1}$	$120^{0} 00^{0}$	0.50	0.18	65.00	4.00	89.06	
63	L106	$59^{0} 42^{1}$	$110^{0} 21^{0}$	8.00	1.02	8.00	2.00	28.55	
64	L107	$59^{0} 43^{1}$	$110^{0} 02^{0}$	14.10	2.72	4.00	1.00	31.11	
65	L108	$59^{0} 28^{1}$	$110^{0} 29^{0}$	1.20	3.41	30.00	4.00	46.36	
66	L109	$59^{0} 07^{1}$	$110^{0} 49^{0}$	5.40	3.15	10.00	2.00	25.62	
67	L75	$59^{0} 35^{1}$	$116^{0} 00^{0}$	0.90	0.29	70.00	2.00	20.74	
68	L82	$59^{0} 26^{1}$	$116^{0} 35^{0}$	0.90	0.28	165.00	6.00	86.62	
69	Steele	$54^{0} 39^{1}$	$113^{0} 46^{0}$	6.10	6.61	154.70	12.80	170.00	
70	Mcleod	$54^{0} 18^{1}$	$115^{0} 39^{0}$	10.70	3.73	22.10	9.50	134.30	
71	Long	$54^{0} 26^{1}$	$112^{0} 45^{0}$	28.00	1.62	62.50	17.80	234.70	
72	Moose	$54^{0} 14^{1}$	$110^{0} 55^{0}$	19.80	40.80	39.00	44.60	329.14	
73	Muriel	$54^{0} 08^{1}$	$110^{0} 41^{0}$	10.70	64.10	32.00	115.00	703.00	*
74	Tucker	$54^{0} 32^{1}$	$110^{0} 36^{0}$	7.50	6.65	49.00	34.00	268.00	
75	Bonnie	$54^{0} 09^{1}$	$111^{0} 52^{0}$	6.10	3.77	41.00	43.00	345.50	
76	Buck	$53^{0} 00^{1}$	$114^{0} 45^{0}$	12.20	25.40	61.00	6.00	125.30	
77	Crimson	$52^{0} 27^{1}$	$115^{0} 02^{0}$	9.10	2.32	17.40	18.00	161.50	
78	Sandy	$53^{0} 47^{1}$	$114^{0} 02^{0}$	4.40	11.40	330.00	7.80	341.50	*
79	Wabamun	$53^{0} 33^{1}$	$114^{0} 36^{0}$	11.00	81.80	36.30	14.90	238.50	

Table IV-2. Continued.

80	Pigeon	$53^{0} 01^{1}$	$114^{0} 02^{0}$	9.10	96.70	33.00	11.60	175.40	
81	Dillberry	$52^{0} 35^{1}$	$110^{0} 00^{0}$	10.70	0.80	16.80	27.30	230.00	
82	Buffalo	$52^{0} 28^{1}$	$112^{0} 54^{0}$	6.50	93.50	79.00	85.00	1235.00	*
83	Gull	$52^{0} 34^{1}$	$114^{0} 00^{0}$	8.00	80.60	49.00	64.50	714.30	
84	Sylvan	$52^{0} 18^{1}$	$114^{0} 06^{0}$	18.30	42.80	20.00	36.00	376.60	
85	Amisk	$54^{0} 35^{1}$	$112^{0} 37^{0}$	60.00	2.82	33.10	18.21	199.50	*
86	Coal	$53^{0} 08^{1}$	$113^{0} 21^{0}$	5.50	10.90	72.90	12.00	215.67	
87	Sturgeon	$55^{0} 06^{1}$	$117^{0} 32^{0}$	9.50	49.10	62.30	5.50	99.80	
88	Moonshine	$55^{0} 53^{1}$	$119^{0} 13^{0}$	3.50	0.28	209.00	38.25	201.30	
89	Crooked	$54^{0} 55^{1}$	$113^{0} 33^{0}$	8.50	1.09	65.00	13.88	0.00	*
90	Jenkins	$54^{0} 55^{1}$	$113^{0} 36^{0}$	15.00	1.46	36.90	12.72	0.00	*
91	Lofty	$54^{0} 43^{1}$	$112^{0} 28^{0}$	5.00	0.67	150.00	0.00	0.00	*
92	Baptiste	$54^{0} 45^{1}$	$113^{0} 33^{0}$	27.50	9.81	47.20	12.15	191.00	*
93	Pine	$52^{0} 04^{1}$	$113^{0} 27^{0}$	12.20	3.89	87.00	24.50	362.40	
	Minimum			0.50	0.18	4.00	0.00	0.00	
	Maximum			60.00	96.70	410.00	158.00	1235.00	
	Mean			5.90	9.53	73.06	12.73	123.61	
	Median			2.20	1.61	61.00	5.00	70.76	
	SD			8.36	20.41	64.55	23.38	172.29	

Table IV-3. Summary of the 10 environmental variables for the 80 lakes used in the final CCA analysis (* indicates at detection limit). Variable names in bold were identified through forward selection to explain significant species variation.

Environmental Variable	Units	Minimum	Maximum	Mean	Standard Deviation	Median
Water Depth	m	0.5	28.0	5.1	5.9	2.0
Lake Area	km^2	0.2	96.7	8.7	18.6	1.6
pH	units	5.2	9.6	7.9	0.8	7.9
Potassium	mg/l	0*	22.5	2.5	4.3	0.8
Calcium	mg/l	0*	68.0	19.0	13.2	17.0
Magnesium	mg/l	0*	158.0	10.9	20.2	4.5
Bicarbonate	mg/l	0*	714.0	106.8	110.2	71.0
Chloride	mg/l	0*	18.3	2.7	4.0	0.9
Sulphate	mg/l	0*	586.0	25.7	72.6	7.0
Total Phosphorus	µg/l	4.0	410.0	72.8	61.1	62.4

Table IV-4. Results of the final Canonical Correspondence Analysis performed on 80 lakes and 10 environmental variables. Rare species were downweighted. (* indicates significant at $p < 0.05$, ** $p < 0.01$). Variables that explained significant proportions of species variation (identified through forward selection) are listed in bold.

Environmental Variable	Canonical Coefficients axis 1	Canonical Coefficients axis 2	t-values of Canonical Coefficients axis 1	t-values of Canonical Coefficients axis 2	Intraset Correlations axis 1	Intraset Correlations axis 2
Depth	1.09	-0.67	**9.43	**-4.27	0.88	0.04
Area	0.00	0.38	0.03	*2.69	0.67	0.24
pH	-0.05	0.16	-0.50	1.10	0.44	0.54
Potassium	-0.28	0.44	-1.68	1.96	0.52	0.58
Calcium	-0.07	0.55	-0.40	*2.4	0.30	0.61
Magnesium	-0.10	0.84	-0.47	*2.86	0.46	0.79
Bicarbonate	0.49	-0.88	1.98	*-2.62	0.54	0.65
Chloride	0.00	0.25	0.05	1.98	0.04	0.65
Sulphate	0.06	-0.19	0.52	-1.17	0.31	0.49
TP	0.48	-0.46	**4.98	**-3.42	0.00	-0.14

Table IV-5. List of species numbers, names, actual and effective number of occurrences (N2), and maximum relative abundance in the 80 lake data set. Presence of species in lakes from 5 different locations in Alberta is indicated (✓). Location areas correspond to: I=Northeast (1-34, 63-66); II=Caribou Mountains area (35-44, 67 & 68); III=Buffalo Head Hills area (45-59); IV=West (60-62, 87 & 88; V=Central (69-86 & 93). Numbers in brackets correspond to lakes (Fig. IV-1) from those areas.

Species Number	Species Name	No. of occur.	N2	Max. Abun. (%)	Location in Province I	II	III	IV	V
1	*Achnanthes conspicua* Mayer	11	3.38	22	✓	✓	✓	✓	✓
4	*A. lanceolata* (Brébisson) Grunow	22	16.00	5	✓	✓	✓	✓	✓
6	*A. linearis* (W.Smith) Grunow	12	11.27	2	✓	✓	✓	✓	
7	*A. minutissima* Kützing	16	7.87	10	✓	✓	✓	✓	✓
8	*A. peragallii* Brun & Heribaud	2	2.00	1	✓			✓	
9	*A. suchlandtii* Hustedt	11	8.40	4	✓		✓		✓
11	*A. subatomoides* (Hustedt) Lange-Bertalot	10	5.54	7	✓		✓		
12	*Amphora libyca* Ehrenberg	27	6.25	33	✓	✓	✓	✓	✓
13	*A. pediculus* (Kützing) Grunow	23	14.56	9	✓	✓	✓	✓	✓
14	*Anomoeoneis serians* (Brébisson) Cleve	2	2.00	1	✓			✓	
16	*A. vitrea* (Grunow) Ross	8	4.00	7		✓		✓	✓
17	*Asterionella formosa* Hassall	28	16.02	16	✓	✓	✓	✓	✓
19	*Aulacoseira ambigua* (Grunow) Simonsen	41	21.16	36	✓	✓	✓	✓	✓
20	*A. distans* (Ehrenberg) Simonsen	5	3.52	11	✓		✓		
21	*A. granulata* (Ehrenberg) Simonsen	17	8.25	55	✓	✓			
22	*A. italica* (Ehrenberg) Simonsen	20	6.50	23	✓	✓	✓		
23	*A. lirata* (Ehrenberg) Ross	2	1.80	2	✓				
25	*Caloneis bacillum* (Grunow) Cleve	2	2.00	1	✓				
26	*C. silicula* (Ehrenberg) Cleve	2	2.00	1	✓			✓	
27	*Cocconeis disculus* (Schumann) Cleve	5	4.50	2	✓				✓
28	*C. neodiminuta* Krammer	4	3.00	4	✓	✓	✓		✓
29	*C. placentula* Ehrenberg	27	4.64	55	✓	✓	✓	✓	✓

Table IV-5. Continued.

30	*Cyclotella distinguenda* Hustedt	8	3.18	26	✓			✓	✓
31	*C. hakanssoniae* Wendker	5	2.13	32	✓	✓		✓	
32	*C. meneghiniana* Kützing	7	4.50	6	✓	✓	✓		✓
33	*C. pseudostelligera* Hustedt	12	4.34	29	✓	✓			✓
34	*C. radiosa* (Grunow) Lemmermann	15	9.71	12	✓	✓		✓	✓
35	*C. stelligera* Cleve & Grunow	26	7.61	30	✓	✓	✓		
36	*C. tripartita* Håkansson	3	1.26	16	✓		✓		
38	*Cymbella amphicephala* Naegli	4	4.00	1	✓	✓			
39	*C. cesatii* (Rabenhorst) Grunow	5	4.63	5	✓			✓	✓
41	*C. gracile* (Ehrenberg) Kützing	4	4.00	1	✓			✓	
42	*C. microcephala* Grunow	12	3.70	17	✓	✓	✓	✓	✓
44	*C. silesiaca* Bleisch	10	7.26	4	✓	✓	✓	✓	
46	*Diploneis occulata* (Brébisson) Cleve	3	2.27	1			✓	✓	
51	*Epithemia argus* (Ehrenberg) Kützing	2	2.00	1		✓			
53	*E. zebra* (Ehrenberg) Kützing	1	1.00	1				✓	
56	*Eunotia bilunaris* (Ehrenberg) Mills	2	1.80	2		✓			
57	*E. exigua* (Brébisson) Rabenhorst	1	1.00	1	✓				
60	*Eunotia intermedia*	2	1.38	5	✓	✓			
62	*E. meisteri* Hustedt	1	1.00	4	✓				
64	*E. pectinalis* (Dillwyn) Rabenhorst	1	1.00	1	✓				
69	*Fragilaria brevistriata* Grunow	50	21.46	58	✓	✓	✓	✓	✓
70	*F. capucina* Desmazières	22	10.75	22	✓	✓	✓		✓
71	*F. capucina* (Rabenhorst) Rabenhorst *v. mesolepta*	4	2.03	25		✓	✓		✓
72	*F. constricta* Ehrenberg	1	1.00	2	✓				
73	*F. construens v. binodis* (Ehrenberg) Grunow	2	2.00	1			✓		
74	*F. construens v. construens* (Ehrenberg) Grunow	39	15.80	34	✓	✓	✓	✓	✓
75	*F. construens v. exigua* (W. Smith) Schultz	1	1.00	1	✓				
76	*F. construens* (Ehrengerg) Grunow *v. venter*	68	41.07	76	✓	✓	✓	✓	✓
77	*F. crotonensis* Kitton	25	12.29	30	✓	✓	✓	✓	✓

Table IV-5. Continued.

78	*F. elliptica* Schumann	6	6.00	1	✓	✓	✓		
81	*F. leptostauron v. martyi* (Heribaud) Lange-Bertalot	22	12.74	9	✓	✓	✓	✓	✓
82	*F. nanana* Lange-Bertalot	8	4.14	15	✓	✓	✓	✓	✓
84	*F. parasitica* (W. Smith) Grunow	5	2.38	2	✓	✓	✓	✓	
85	*F. pinnata* Ehrenberg	70	33.68	61	✓	✓	✓	✓	✓
87	*F. vaucheriae* (Kützing) Petersen	2	2.00	1	✓		✓		
88	*F. virescens* Ralfs	10	6.72	8	✓	✓	✓		
89	*Frustulia rhomboides* (Ehrenberg) De Toni	2	1.47	4	✓	✓			
91	*Gomphonema angustum* Agardh	3	2.27	3		✓			
92	*G. angustatum* (Kützing) Rabenhorst	2	1.96	4		✓	✓		
94	*G. gracile* Ehrenberg	3	2.27	3		✓	✓		
96	*G. minutum* (Agardh) Agardh	13	10.71	3	✓	✓	✓	✓	✓
97	*G. parvulum* (Kützing) Kützing	8	7.36	2		✓	✓	✓	
99	*Navicula absoluta* Hustedt	2	1.80	2		✓	✓		
100	*N. bergerii* Krasske	1	1.00	4			✓		
101	*N. capitata* Ehrenberg	6	1.58	40			✓	✓	
104	*N. cuspidata* (Kützing) Kützing	7	6.40	1	✓	✓		✓	
105	*N. cryptotenella* Lange-Bertalot	5	1.65	46		✓		✓	✓
107	*N. digitulus* Hustedt	2	1.80	2		✓			
108	*N. elginensis* (Gregory) Ralfs	6	4.50	4	✓	✓	✓	✓	
109	*N. halophila* (Grunow) Cleve	1	1.00	1	✓				
110	*N. harderii* Hustedt	5	2.79	5		✓	✓	✓	
111	*N. jaernefeltii* Hustedt	2	2.00	3	✓				
112	*N. mediocris* Krasske	4	3.57	2	✓	✓			
114	*N. minima* Grunow	4	2.58	4		✓		✓	
115	*N. laevissima* Kützing	20	4.50	46	✓	✓	✓	✓	
116	*N. lanceolata* (Agardh) Ehrenberg	2	2.00	1	✓			✓	
117	*N. leptostriata* Jørgensen	10	5.14	17	✓	✓	✓	✓	
118	*N. gallica v. perpusilla* (Grunow) Lange-Bertalot	1	1.00	2	✓				

Table IV-5. Continued.

119	*N. pseudoscutiformis* Hustedt	3	3.00	1	✓		✓		
120	*N. pseudoventralis* Hustedt	4	3.20	3		✓	✓		✓
121	*N. pupula* Kützing	24	17.00	4	✓	✓	✓	✓	✓
122	*N. radiosa* Kützing	24	9.08	18	✓	✓	✓		
123	*N. recens* (Lange-Bertalot) Lange-Bertalot	3	3.00	1	✓		✓		
125	*N. seminulum* Grunow	4	3.57	2	✓	✓	✓		
126	*N. soehrensis* Krasske	2	2.00	1	✓	✓			
127	*Neidium affine* (Ehrenberg) Pfitzer	3	2.22	9	✓	✓			
128	*N. apiculatum* Reimer	1	1.00	1	✓				
129	*N. bisulcatum* (Lagerstedt) Cleve	2	1.80	2	✓		✓		
130	*N. iridis* (Ehrenberg) Cleve	4	4.00	1	✓		✓	✓	
132	*Nitzschii amphibia* Grunow	14	7.71	18		✓	✓	✓	✓
133	*N. fonticola* Grunow	12	3.61	42	✓	✓	✓	✓	✓
134	*N. heufleriana* Grunow	2	1.60	3		✓		✓	
135	*N. linearis* (Agardh) W.Smith	4	2.63	17	✓	✓	✓		
136	*N. palea* (Kützing) W.Smith	11	8.52	5	✓	✓	✓	✓	✓
137	*N. paleacea* Grunow	4	2.88	7		✓		✓	✓
139	*Pinnularia biceps* Gregory	5	5.00	1	✓		✓		
141	*P. gibba* Ehrenberg	2	2.00	1	✓				
143	*P. mesolepta* (Ehrenberg) W.Smith	3	2.67	2	✓	✓	✓		
145	*P. subcapitata* Gregory	2	2.00	1		✓		✓	
146	*P. viridis* (Nitzsch) Ehrenberg	3	2.67	2	✓		✓		
147	*Rhopalodia gibba* (Ehrenberg) O.Müller	3	2.67	1		✓		✓	
148	*Stauroneis anceps* Ehrenberg	7	5.56	3	✓		✓	✓	
151	*Stephanodiscus hantzschii* Grunow	1	1.00	2	✓				
152	*S. niagarae* Ehrenberg	33	10.92	41	✓	✓	✓	✓	✓
153	*S. parvus* Stoermer & Håkansson	32	15.42	61	✓	✓	✓	✓	✓
156	*Tabellaria flocculosa* (Roth) Kützing strain IV *sensu* Koppen	11	7.51	6	✓	✓	✓	✓	
157	*T. flocculosa* (Roth) Kützing strain IIIp *sensu* Koppen	22	10.46	21	✓	✓	✓		✓

Table IV-5. Concluded.

158	*Tetracyclus lacustris* Ralfs	5	4.45	2	✓	
160	*Navicula cf. mediocris* Krasske	7	6.40	2	✓	✓
162	*N. cf. submuralis* Hustedt	12	7.23	6	✓	✓

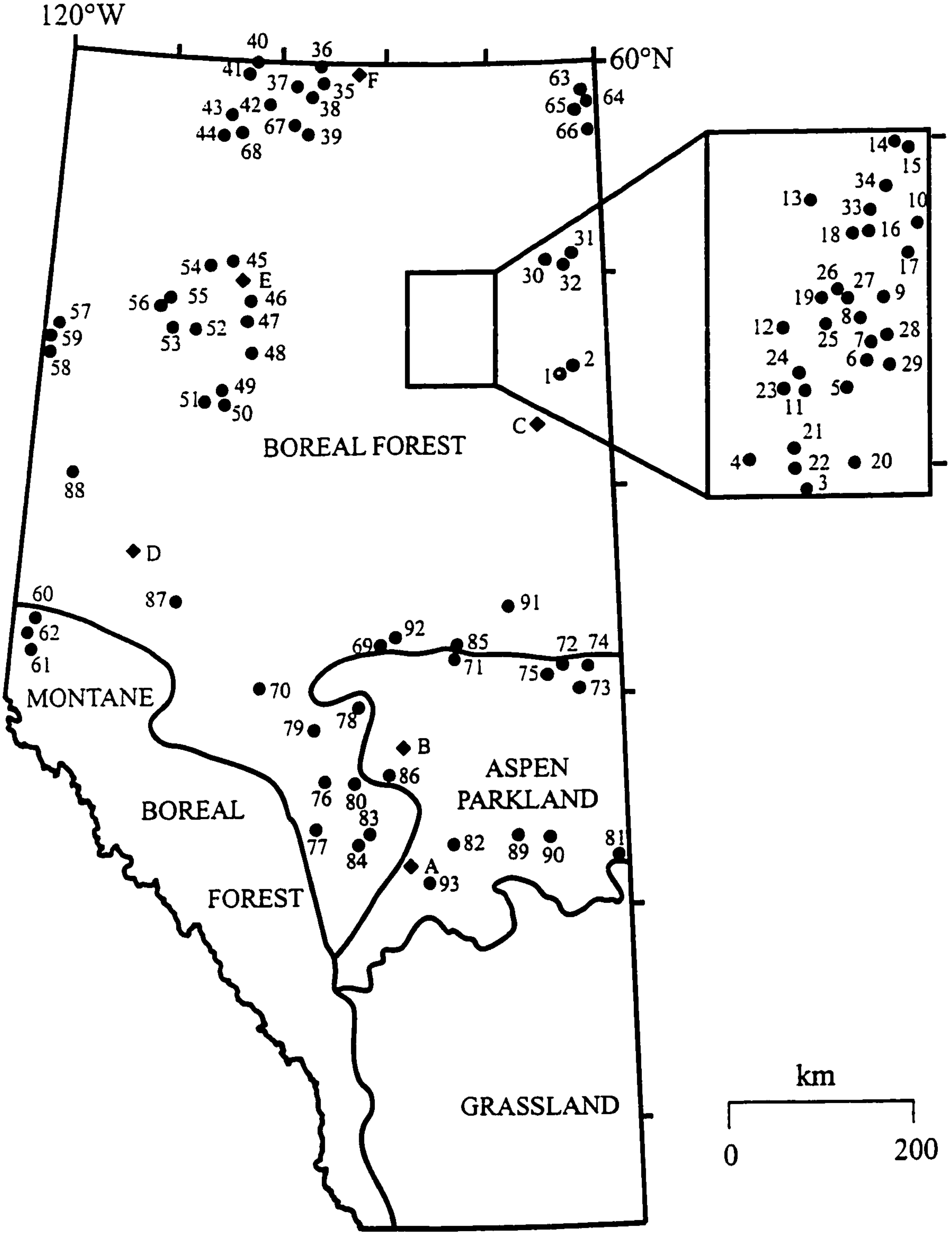


Figure IV-1. Map of the province of Alberta indicating the location of the 93 lakes (●) and 6 climate stations (◆).

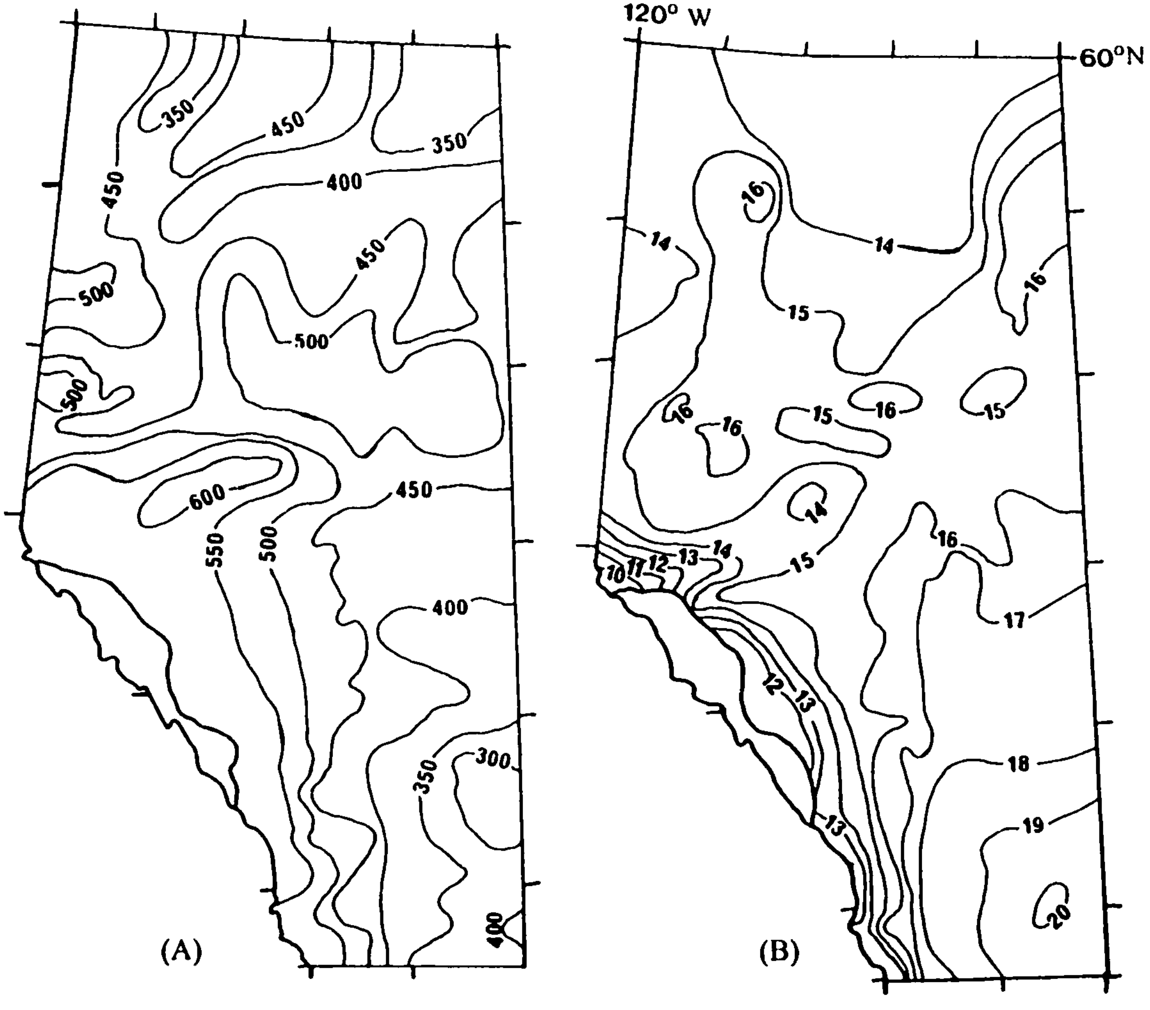


Figure IV-2. General climate of Alberta as summarized by (A) total annual precipitation (mm) and (B) mean July temperature (degree C). Modified from Atlas of Alberta (1984).

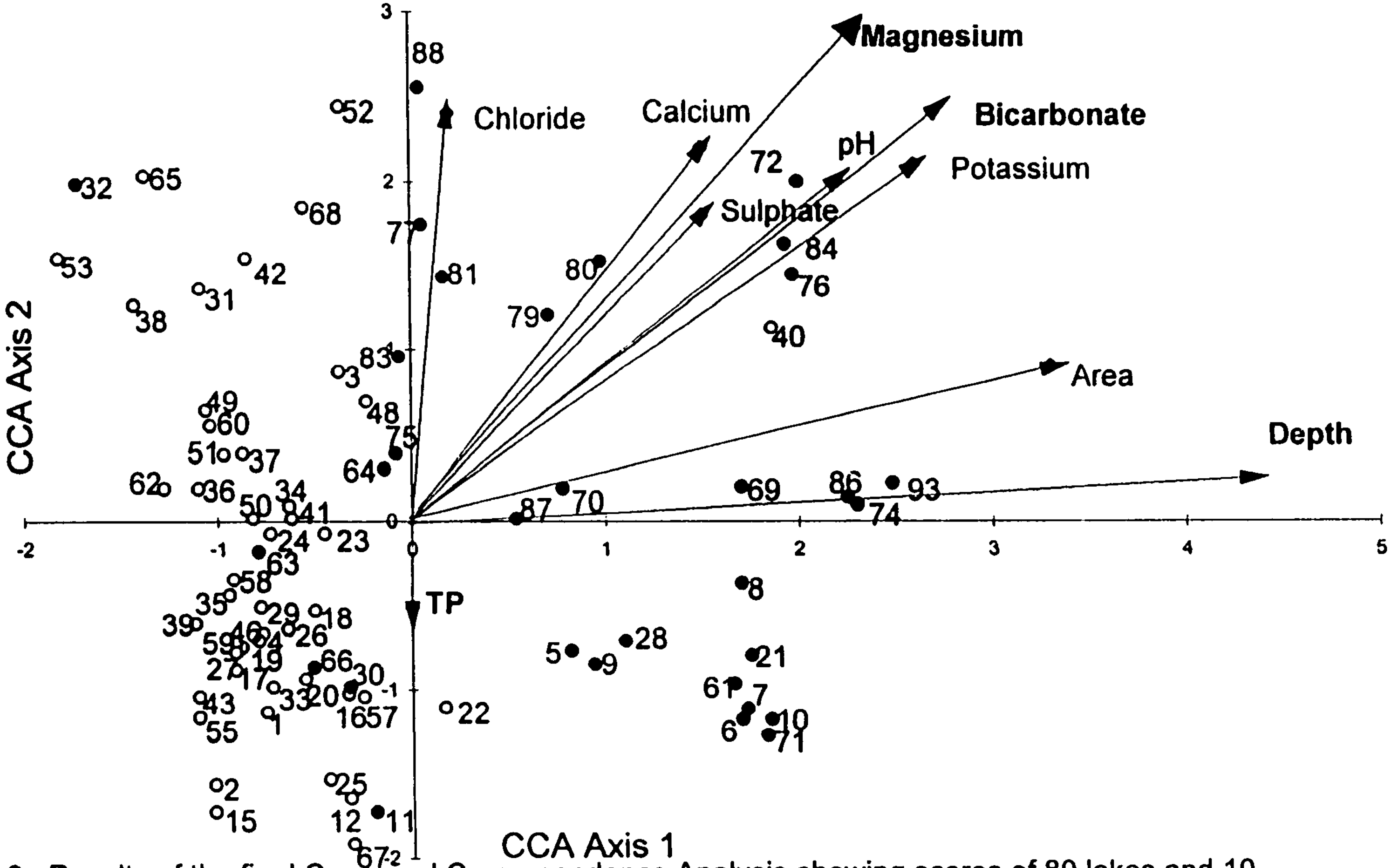


Fig. IV-3. Results of the final Canonical Correspondence Analysis showing scores of 80 lakes and 10 environmental variables. Scores of environmental variables were magnified 10-fold. Deep (●) and shallow (o) lakes of the data set are indicated.

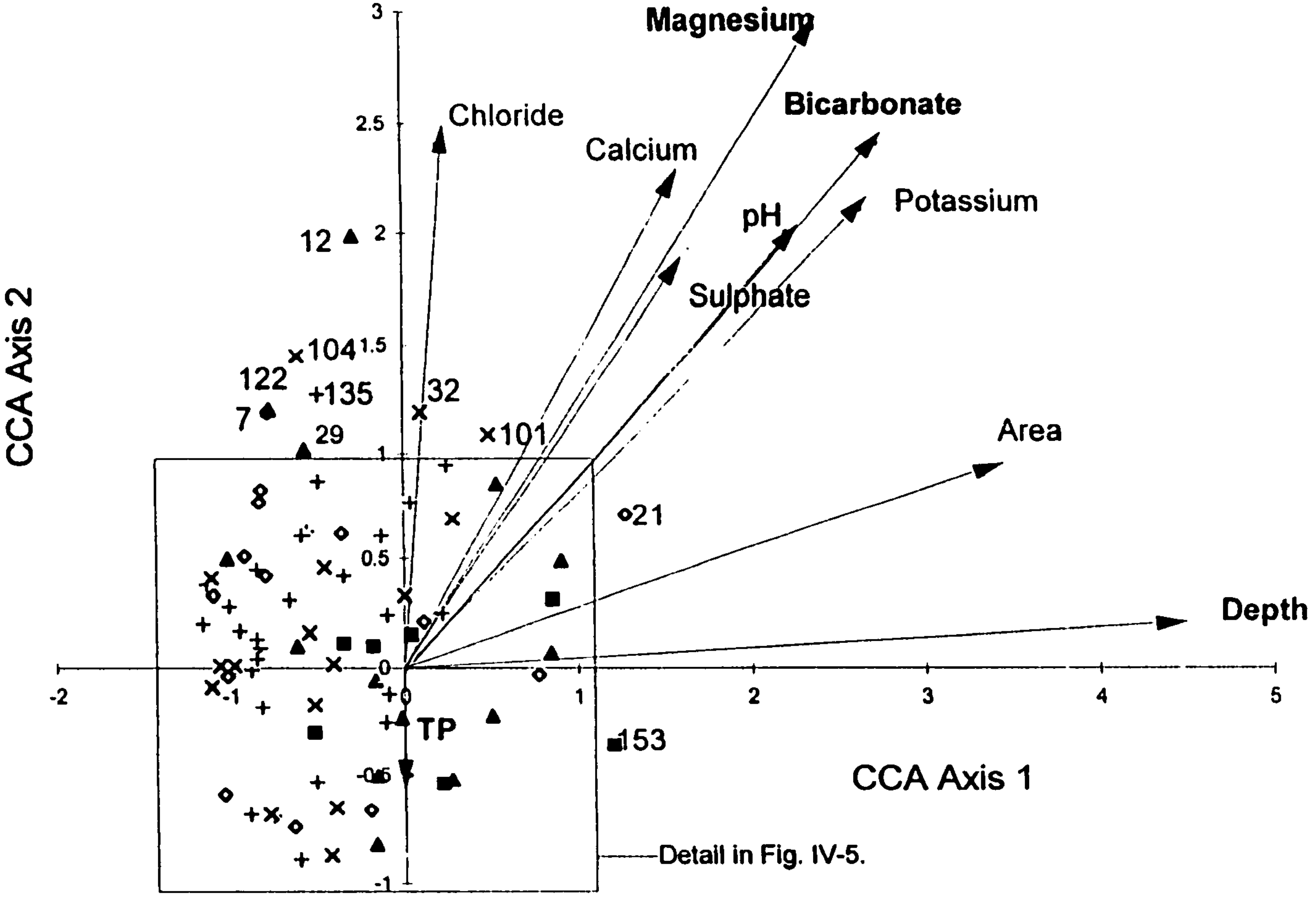


Fig. IV-4. Final Canonical Correspondence Analysis results showing scores of 80 diatom species (>2 occurrences) and trajectory arrows of 10 environmental variables. Scores of environmental arrows were magnified 10-fold. Symbols indicate number of occurrences in the 80 lakes (+: 3 to 5 lakes; x: 6 to 10 lakes; ◇: 11 to 19 lakes; ▲: 20 to 30 lakes; ■: > 30 lakes).

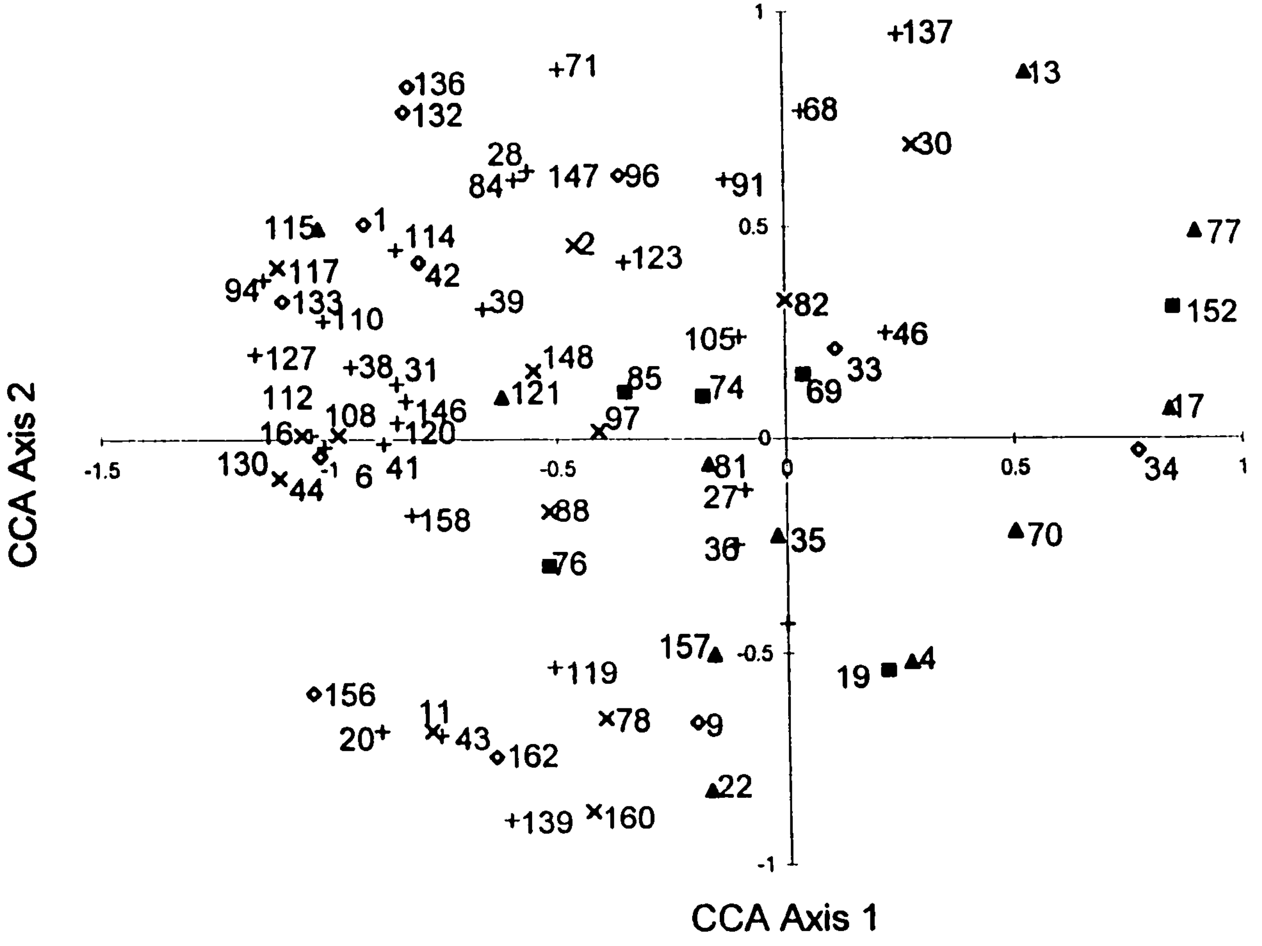


Fig. IV-5. Results of final Canonical Correspondence Analysis (CCA) showing scores of 70 diatom species (> 2 occurrences) between -1.5 to 1.0 on the x-axis and -1.0 to 1.0 on the y-axis.

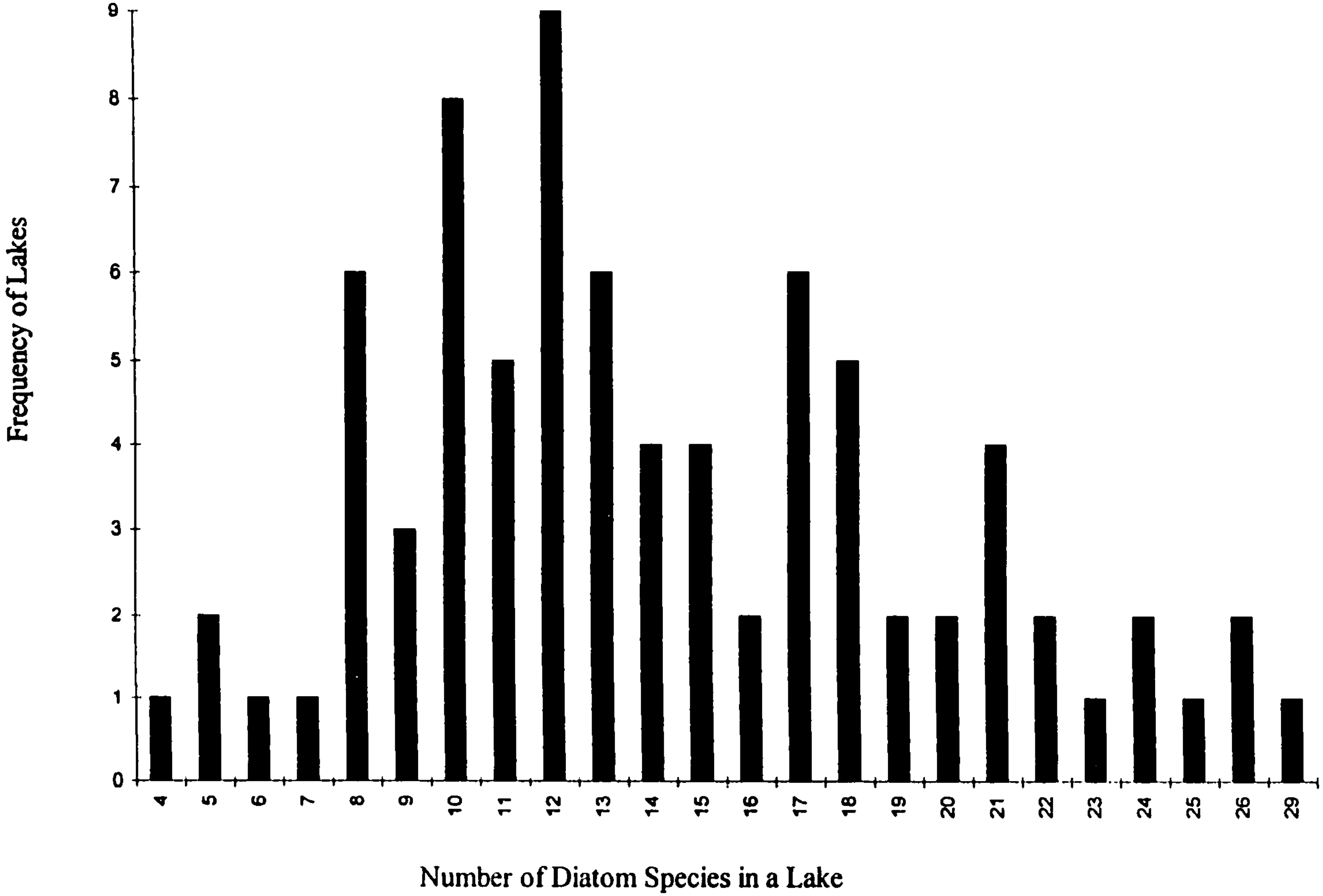


Fig. IV-6. The frequency distribution of the number of diatom species found in 80 Alberta lakes.

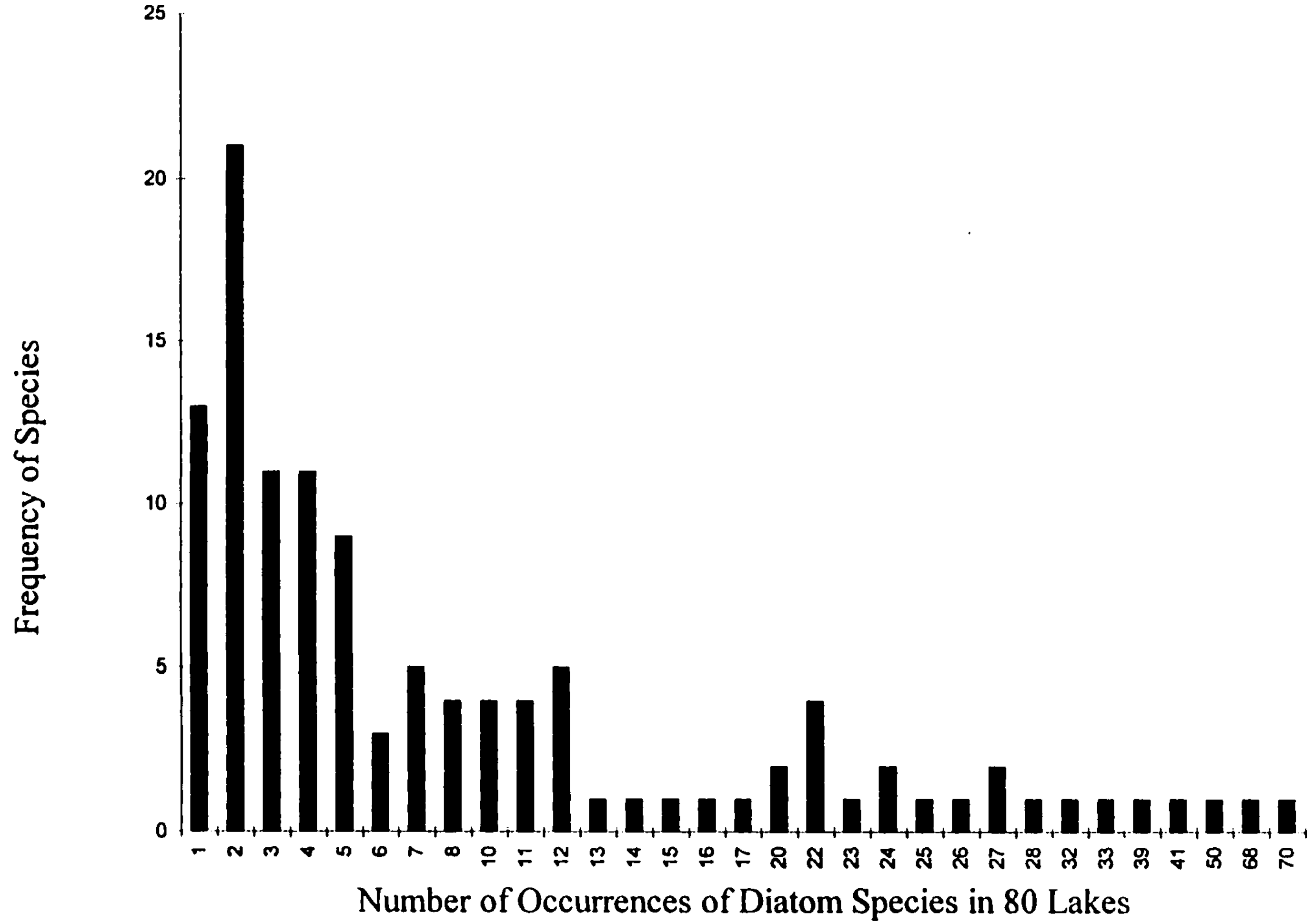


Fig. IV-7. Frequency distribution of the number of occurrences of each diatom species in the 80 Alberta lakes.

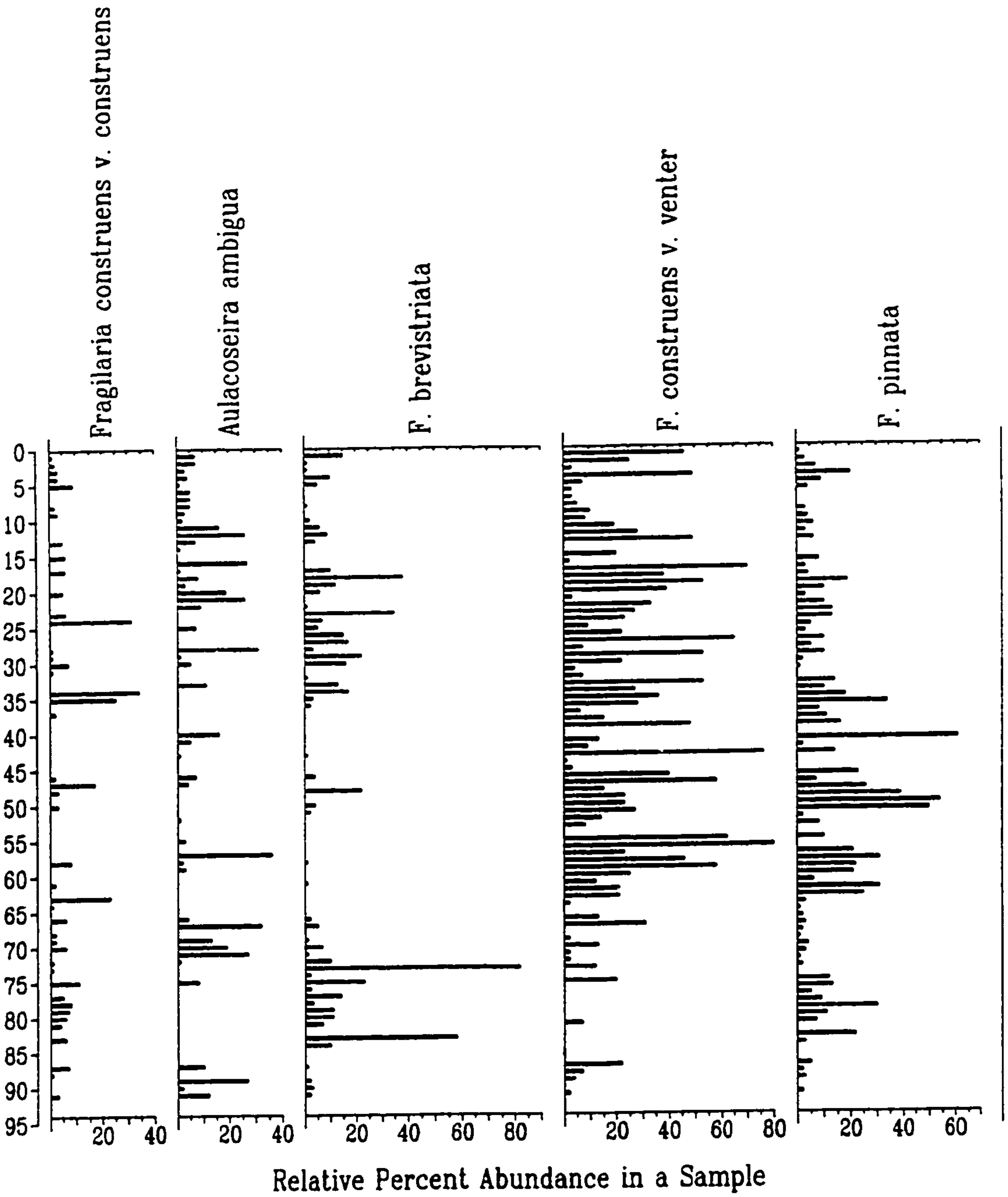
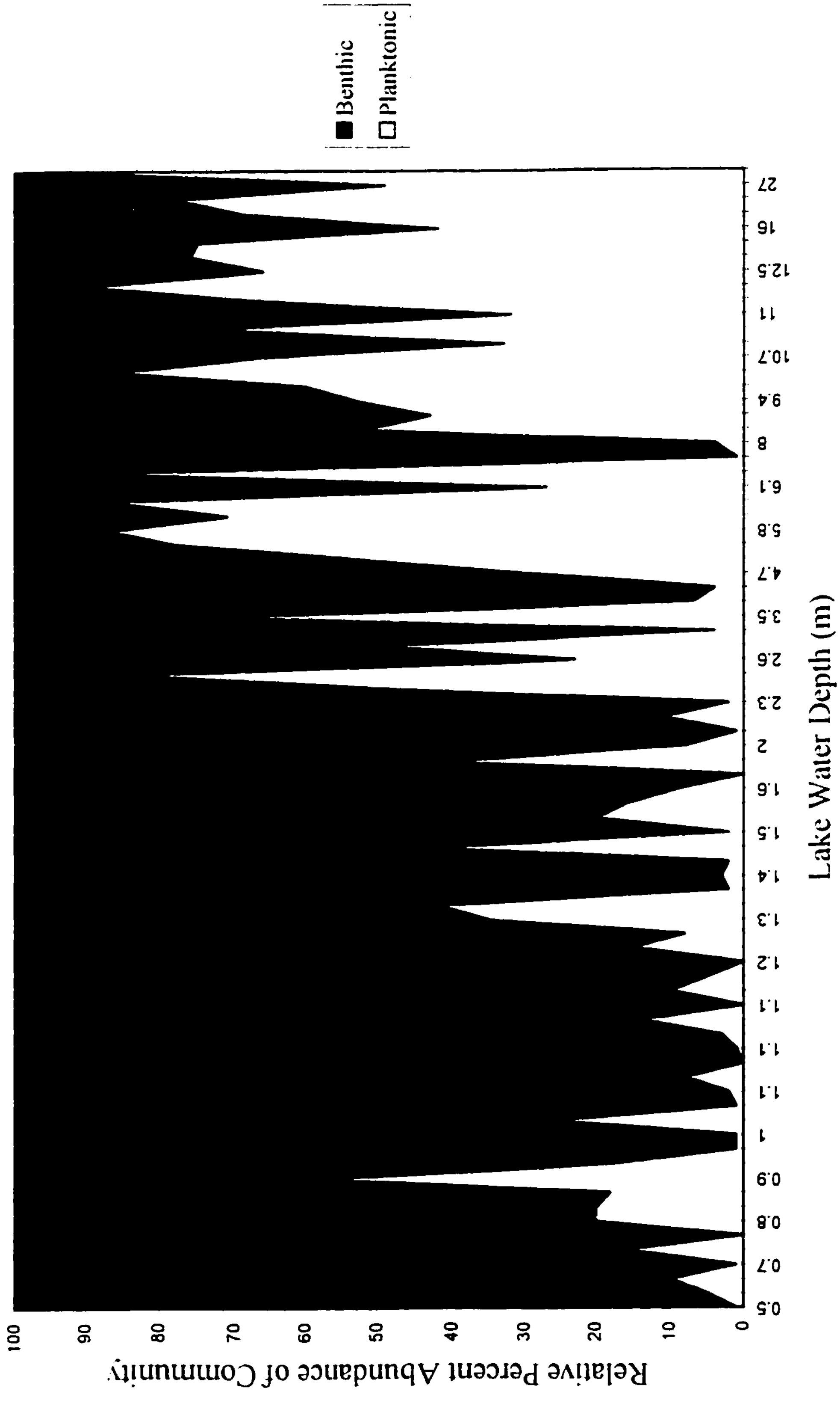


Figure IV-8. The relative percent abundance of the 5 most common diatom species in the 80 lake data set.


■ Benthic
□ Planktonic
Relative Percent Abundance of Community
0
10
20
30
40
50
60
70
80
90
100
Lake Water Depth (m)
0.5
0.7
0.8
0.9
1
1.1
1.1
1.1
1.2
1.3
1.4
1.5
1.6
2
2.3
2.6
3.5
4.7
5.8
6.1
8
9.4
10.7
11
12.5
16
27

Chapter V. A model developed from Alberta Lakes to infer Total Phosphorus (TP) concentration from sedimentary diatom assemblages.[1]

V.A. Introduction

Freshwater diatoms (Bacillariophyceae) are widely distributed in the biosphere, they form significantly large assemblages in aquatic habitats, and they are sensitive to various environmental factors. Due to their siliceous cell walls, they preserve exceptionally well in most lacustrine sediments. Short or long-term accumulations of diatom assemblages are analyzed by palaeolimnologists to describe lake development. Initial studies of diatom assemblages and their relationship to environmental variables were undertaken before the advent of multivariate statistical approaches, and they were therefore descriptive (e.g. Kolbe, 1927; Hustedt, 1930, 1937-1939; Round, 1959, 1964; Round & Brooks, 1959). Investigations using statistical methods have demonstrated that diatom assemblages are strongly, and significantly related to lake water pH (e.g., Birks *et al.*, 1990; Flower, 1986), salinity (e.g., Fritz *et al.*, 1991; Cumming & Smol, 1993; Wilson *et al.*, 1996), dissolved organic carbon (e.g., Pienitz & Smol, 1993) and nutrients (e.g., Whitmore, 1989; Agbeti, 1992; Hall & Smol, 1992; Fritz *et al.*, 1993; Christie & Smol, 1993; Bennion, 1994; Reavie *et al.*, 1995). Quantitative inference models derived from these investigations are applied to palaeolimnological records to answer questions regarding acidification, climate change and eutrophication (Anderson, 1994).

Calibration sets used to develop inference models are developed from a series of lakes. From these lakes, surficial sedimentary diatom assemblages and lake environmental data are collected. It is assumed that one sample from the surficial sediments will contain a representation of species that have occurred in all habitats of the lake over the previous few years (Dixit *et al.*, 1995). Environmental data recorded from the lake includes water chemistry and physical parameters of the lake and catchment. Lakes may be chosen to fit along a gradient of a predefined variable, or they may be randomly selected. It is assumed that diatom species are significantly related to either the predefined variable, or one of the other measured environmental variables. Through the use of multivariate statistical

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[1] A version of this chapter has been submitted to Freshwater Biology. Prather & Hickman.

approaches (ter Braak & Prentice, 1988), variables that significantly influence species distributions are determined, and then through calibration statistics, species optima and tolerances for a variable are determined (ter Braak & van Dam, 1989).

This study was undertaken to analyze the relationship between diatom species and chemical and physical parameters of some deep lakes in Alberta. The relationship between diatom and lake chemical and physical parameters from a large number of lakes in Alberta has already been determined (Chapter IV.). From that analysis, depth of the lake water was determined to be an overriding factor in influencing diatom species assemblages. A subset of deeper lakes was chosen from the large data set. The use of deep lakes only removes the underlying influence of algal community, which is largely influenced by depth of the water, and area of substrate available for colonization. It also allows a better investigation into the relationship between diatom species and water chemistry. The first objective of this study was to analyze the subset of deeper lakes, and determine which aspects of water chemistry significantly influenced diatom species assemblages. Lakes with maximum water depth greater than 3.5 m were included. It was hypothesized that significant relationships between species and environmental variables would be determined even though there was no predefined environmental gradient for a specific variable. In addition, two lakes with water depth less than 3.5 m, but high planktonic populations were included in the analyses. Excess nutrients can stimulate planktonic algae (Schindler, 1985), and inadvertently change the community structure in a lake or pond. These two shallow lakes were included in this study to observe the similarity between planktonic populations of deep and shallow lakes.

Data sets have been collected from British Columbia (Hall & Smol, 1992; Cumming & Smol, 1993; Reavie *et al.*, 1995; Wilson *et al.*, 1996), northern Canada (Pienitz & Smol, 1993), Ontario (Christie & Smol, 1993; Agbeti, 1992), Michigan (Fritz *et al.*, 1993), Canadian and northern United States prairie region (Fritz, 1990; Fritz *et al.*, 1991), Florida (Whitmore, 1989), and various locations in Europe (e.g., Birks *et al.*, 1990; Anderson *et al.*, 1993; Bennion, 1994). Data sets are collected from the different areas because there are regional variations in geology, climate, soils and vegetation that may influence species assemblages. For example, changes in catchment vegetation influence lake-quality, and algal species assemblages (Hall & Smol, 1993; Hickman & Reasoner, 1994, 1998; Hickman & Schweger, 1996). It was hypothesized that the relationship between diatom species and water chemistry would vary between areas due to differences in geology, climate, soils and vegetation. These factors have an influence upon lakes and biota, and may be revealed by the specific relationship between species and water chemistry in separate calibration sets.

The second objective was to derive a statistical model for the variable(s) that significantly influenced diatom species distributions. The best model would be determined by analyzing root mean squared error (RMSE) of prediction values (Wallach & Goffinet, 1989), correlation coefficients between observed and inferred values, and trends in plots of residual values (Birks *et al.*, 1990). By applying the model to the diatom species assemblages at various horizons in the sediment cores, the rate and magnitude of change of the particular variable over time can be estimated. These quantitative reconstructions of lake history can be of use to lake managers when determining courses of action for lake remediation.

V.B. Site Description

The province of Alberta is divided into several ecoregions. These are defined primarily by geographic and climatic features (Crosby, 1990) because these influence the vegetation and soils, that develop in an area. The ecoregions of Alberta have been mapped and described by Strong and Leggat (1981). This map has been summarized, and the location of the 42 lakes within these regions are indicated (Fig. V-1). Also indicated on this figure are the climate stations (A-F). Detailed information, based on 30-year climate normals (Atmospheric Environment Service, 1993), for each of these stations is given (Table V-1). Annual total precipitation (mm) (Fig. V-2a) and mean July temperature (°C) (Fig. V-2b) for the province has been summarized (Atlas of Alberta, 1984). The annual total precipitation in the northern to central regions is generally higher than in the southern regions. Northern Alberta, along with mountain and foothills regions, experience cooler summer temperatures than the southern portion of the province. As a result dense forest tends to develop in the northern, mountain and foothills regions, open parkland to grasslands tend to develop in the central region, and dry grassland tends to develop in the southern region (Fig. V-1).

Much of the vegetation of the Boreal Forest consists of trees including *Betula balsamifera, Populus tremuloides, Pinus banksiana, Picea glauca,* and *P. mariana.* The importance of each tree species in the catchment of a lake is influenced in general by precipitation, evaporation and soil type. Wetlands and peatlands also occur in the Boreal Forest region, and in some areas, open peatlands, as opposed to dense forests, occur over large areas (Halsey *et al.*, 1997). The Montane Boreal Forest typically has *Pinus banksiana, Picea glauca,* and *P. mariana* as the dominant tree species. Finally, the Aspen Parkland typically has *Populus tremuloides* as the only tree species, combined with a large variety of grass species. This area is typically drier due to more evaporation than the more northerly Boreal Forest. In addition, decomposition rates are generally higher, thus limiting moss accumulation (Zoltai & Vitt, 1990). Stands of trees in the Aspen Parkland can vary from dense forests in the northern and western regions, to open groveland in the southern and eastern portions of this ecoregion. This ecoregion is variable in runoff, and as a result lake levels can vary from year to year (Crosby, 1990).

The Boreal Forest region of Canada (Rowe, 1972) occupies approximately the northern two thirds of the province, and has been divided into five ecoregions by Strong and Leggat (1981). Lakes from this study were found in 4 of these Boreal Forest ecoregions. Most of the lakes sampled (n=23) were located in central Alberta, around the Boreal Forest – Aspen Parkland transition region (Fig. V-1). Some lakes from the extreme north (n=4), northeast (n=12) and extreme west (n=3) were also sampled.

The algal assemblages of two closely adjacent lakes from the same ecoregion can be quite different. Differences may be due to internal lake factors, but also to external lake factors. External influences may include catchment size, degree and type of anthropogenic impact in a catchment, and direct impacts on a lake. These factors, which were not measured or accounted for in this study, could in fact have significant influences upon the diatom assemblage, and the species relationship to the physical and chemical parameters of the lake.

V.C. Methods

V.C.1. Sampling

The lakes (n=36) included in this study were sampled by personal at Alberta Environment and the Limnology Lab, University of Alberta (n=6). Samples for surficial sediments and water chemistry were taken from the deepest part of each lake. Personnel from Alberta Environment sampled lakes once during August 1992 or 1993. Additional lakes were also sampled once during August 1994 by the former plus the senior author. Composite water samples for chemical analysis were collected from 0.5 m below the surface of the water, divided into various bottles for analysis of different chemical variables, and shipped within 10 hours to the Alberta Environmental Centre, Vegreville, for analysis. The uppermost 3 cm of sediment, representing a composite sample of the previous few years, was removed using a Kajak-Brinkhurst (K-B) gravity corer (Glew, 1991). Sediments were placed in plastic containers and stored frozen.

The remaining 6 samples were taken once by personnel from the Limnology Lab, University of Alberta, between June 1991 and August 1993. Composite water samples, collected 0.5m below the surface of the water, were analyzed in the Limnology Lab. The uppermost 1cm of sediment was removed from the deepest part of each lake. Sediments were either stored frozen in plastic bags, or freeze-dried and then stored frozen in plastic bags.

V.C.2. Laboratory Analysis

The frozen sediment samples were allowed to thaw slowly, and then 1 cm^3 subsamples were taken from each and treated with $K_2Cr_2O_7$ and H_2SO_4 to remove all organic matter (Hickman *et al.*, 1984). The diatom slurry was then washed with deionized water until there were no traces of acid. Aliquots of 0.02 - 0.35 mL were pipetted onto coverglasses, air dried slowly to ensure even distribution of valves across the coverglass, and then fixed permanently in Hyrax.

A minimum of 500 diatom valves was counted on each slide at 1000x using oil immersion. Identifications were made using Germain (1981), Hustedt (1930), Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), and Patrick and Reimer (1966, 1975).

Water samples were analyzed for chemical composition at the Water Analysis Laboratory (n=36) (Alberta Environment Lab Manual, 1987) at the Alberta Environmental Centre, or the Limnology Lab (n=6), University of Alberta.

V.C.3. Data Analysis

To derive a model to estimate site environmental variables from species assemblages, species optima for the environmental variable must be calculated. It is assumed that a species will be most abundant when the site value is close to the optimum value for that species (ter Braak & van Dam, 1989).

Diatom samples came from surficial sediments of each lake. These sediments represent the accumulation of matter over a few years. In order to derive predictive equations it is assumed that the diatom species deposited and preserved in these modern sediments are related to and influenced by the environment of the lake (chemistry of the water and morphometry of the basin). Diatom species were tallied as relative percent abundance of total counts in the sample. Diatoms representing ≥ 1% in at least 2 samples were included

Chemistry and lake data were available for 16 variables. These included maximum water depth (depth), lake area (area), pH, conductance , alkalinity, total dissolved solids (TDS), and concentrations of dissolved sodium, potassium, calcium, magnesium, bicarbonate, chloride, sulphate, silica, total phosphorus (TP), and organic carbon. Environmental variables were tested for normality. Several of the variables had positively skewed distributions and they ln(x+1) transformed (Zar, 1984). Variables with skewed distributions that were transformed included depth, area, conductance, alkalinity, TDS, sodium, potassium, calcium, magnesium, bicarbonate, chloride, sulphate and TP. The calibration set included 42 lakes, 16 variables and 86 species.

V.C.3.a. Ordination

Ordination is a statistical method that organizes samples along a hypothetical environmental gradient based upon their species composition (ter Braak, 1987). The computer program CANOCO (version 3.10) (ter Braak, 1990a, 1990b) was used to perform the ordinations. Both indirect and direct ordinations were used. Correspondence Analysis (CA) and the canonical form of CA (CCA) were derived from the weighted averaging method of Whittaker (ter Braak, 1987). A unimodal response of species relative abundance across an environmental gradient is assumed (ter Braak & Looman, 1987). A species will be most abundant at sites where the environmental value is close to the optimal value, and conversely least abundant where the environmental value is very different from the species optimal value.

Indirect ordination arranges species along a hypothetical environmental gradient. Detrended correspondence analysis, DCA, is an example of indirect ordination. When using this method it is assumed that species have a unimodal response along environmental gradients (ter Braak, 1987). When using DCA, the lengths of the ordination axes are estimated. When the axes are long (> 3 standard deviations) then the sites at opposite ends have very few species in common (ter Braak, 1987). Samples with unusual species combinations can be detected by using this method. Samples that lie more than 3 standard deviations from the mean of species scores are detected and deleted. In an ordination diagram these samples are so far removed from the remaining samples that the remaining samples group together, and underlying gradients cannot be inferred.

CCA is a direct ordination method. It too assumes a unimodal response of species to environmental gradients. In canonical ordination the observed environmental variables which can best explain the variation in the species data are determined (ter Braak, 1987). The ordination axes and the site scores are linear combinations of environmental variables (ter Braak, 1987). The result is a maximum of species dispersion. The pattern of species variation, and the relationship between the species and each environmental variable are displayed on the ordination biplots (ter Braak, 1987).

V.C.3.b. Data Screening

The environmental data set was examined for unusual samples, repetitive environmental variables, and environmental variables that did not influence diatom species distributions (Birks *et al.*, 1990). The data screening process outlined below follows the methods of Hall and Smol (1992) and Cumming and Smol (1993).

Outlier samples. Samples may have unusual species assemblages or extreme environmental variables. These can influence the results by grouping samples and not showing underlying gradients in the remaining samples. These outliers were removed in order to determine the most influential variables in the remaining samples. Outlier samples were detected using Detrended Correspondence Analysis (DCA) on the species data. Samples outside the 95% confidence limits were deleted from subsequent analyses.

Redundant environmental variables. A variety of steps were taken to remove superfluous environmental variables and reduce the number to the fewest that would explain most of the variance in the species data. Environmental variables were included if (1) they were not significantly correlated to other variables, or (2) if they were correlated but exerted an independent influence on the species data. The following steps identified any redundant variables.

(1). Groups of significantly correlated variables ($p \leq 0.05$) were determined from a Pearson correlation matrix.

(2). An initial CCA was run (with the outlier samples omitted) using the forward selection option. This determined which variables in each of the above groups explained the most variation in the species data. This variable was used as a representative of the group. Significance of a variable in explaining species variation was determined through Monte Carlo permutation tests (99 unrestricted permutations; $p \leq 0.05$).

(3). To determine if any other correlated variables of a single group had independent influence, a series of partial CCAs were run. The variable identified in the previous step was chosen as the main variable and each correlated variable was selected individually as the sole co-variable. Independent influence of the co-variable was determined by testing the significance of the first canonical ordination axis ($p \leq 0.05$) using a Monte Carlo permutation test with 99 unrestricted permutations. Only those variables with significant influence were retained for further analyses.

(4). Another CCA was run on the dataset with outlier samples and non-significant variables excluded. At this stage variables with high variance inflation factors (VIF > 20) were identified (Cumming & Smol, 1993). These variables have unstable coefficients and do not merit further interpretation (ter Braak, 1986). A series of CCAs were run omitting the variable with the highest VIF in each run until all variables had VIF values less than 20.

After all non-significant variables were removed, the results were checked for extreme samples. Extreme samples may also have unusual diatom assemblages and/or unusual values of environmental variables (Birks *et al.*, 1990), which could alter the results. These samples were not detected as outliers using DCA. Samples which have extreme values for any environmental variable have a large influence (> five times) (Birks *et al.*, 1990). Any sample with an extreme influence in one or more environmental variable was deleted from the final CCA.

A final CCA was run once all outlier samples, non-significant environmental variables, and extreme samples were removed. Forward selection was used to determine the significance of each variable and the amount of variation explained by each variable.

V.C.3.c. Regression and Calibration

Weighted averaging (WA) regression and calibration also assumes a unimodal response between species and environmental variables. In WA regression optimal values are estimated for each species for the selected environmental variable. This is calculated from the occurrence of a species in many samples, and the value of the environmental variable in each sample. WA calibration performs the opposite procedure. The site value for a particular environmental variable is estimated based upon (1) the species composition and (2) the estimated optimum value for each species. The "weight" in WA refers to the relative abundance of a species in a lake (Cumming and Smol, 1993). The computer program WACALIB version 3.3 (Line *et al.*, 1994) was used to perform the regressions and calibrations.

During regression and calibration averages are taken twice and the range of values shrinks. Deshrinking by either inverse or classical methods are used to correct for the shrinkage in range (ter Braak & van Dam, 1989).

The accuracy of prediction of the derived models was determined by the correlation coefficient (between observed and inferred values) (Birks *et al.*, 1990), the apparent root mean squared error (RMSE) of prediction (Wallach and Goffinet, 1989) and the residual plot (observed versus observed-inferred values) (Birks *et al.*, 1990).

V.D. Results

V.D.1. Data Screening

The original data set consisted of 42 samples and 16 environmental variables. There were 40 lakes with maximum water depth greater than 3.5 m. Another two lakes, with shallow water depth (< 3.5 m), were retained because they had high planktonic populations. The species assemblages in these two lakes were determined to be similar to the species found in the deeper lakes (Chapter IV). The location of the lakes and some of the important environmental variables for each lake are listed (Table V-2; Fig. V-1). Data screening was used to remove samples with extreme, or unusual species assemblages and/or extreme values for environmental variables. Detrended Correspondence Analysis (DCA) detected two outlier samples, specifically samples 32 and 82 with unusual species assemblages. Sample 32 had a very low concentration of total phosphorus (TP) (9 µg/L), but more importantly it had an unusual species assemblage. The flora was 96% benthic, and dominated by *Navicula laevissima* (46%). Sample 82 had extremely high conductance (2815 us/cm), alkalinity (1179 mg $CaCO_3$/L), TDS (1951 mg/L), and dissolved ions, in addition to a diatom flora dominated by *Fragilaria capucina v. mesolepta* (> 85%).

Sample 91 has missing values for many of the environmental variables. For many other samples, there were missing values for chloride, dissolved silica, and dissolved organic carbon. Samples 32, 82 & 91 and three environmental variables (chloride, silica, and organic carbon) were deleted from all subsequent analyses.

Canonical Correspondence Analysis (CCA), direct ordination, was run on the data set with the above omissions. From this analysis two variables with high Variance Inflation Factor (VIF > 20) values were detected. High VIF values indicate that the canonical coefficients are unstable, and are not worth further interpretation (ter Braak, 1988). The variable with the highest VIF was omitted, and the CCA was re-run. This continued until all VIF values were less than 20. Conductance and alkalinity had VIF values greater than 20. These 2 variables were omitted from all subsequent analyses.

Another CCA was run to determine groups of significantly correlated variables. Calcium, bicarbonate, sulphate and total phosphorous (TP) were not significantly related to any other variable. Forward selection was also used to identify variables that significantly influenced species distribution. The variables magnesium, calcium, TP, lake area and water depth significantly influenced diatom species distribution. These variables were used as sole variables in a series of partial CCAs. Variables significantly correlated to the former 5 variables were used individually as co-variables in partial CCAs. Using a Monte Carlo permutation test, with 99 unrestricted permutations, the significance of the canonical axis was tested. Those co-variables that added a significant influence ($p \leq 0.05$ on the first axis) were retained, while those that did not were omitted from further analyses. For example, magnesium was significantly correlated to pH, TDS, sodium, potassium, bicarbonate and sulphate. In partial CCAs run separately between magnesium (variable) and each of the other variables (as co-variables) only TDS, bicarbonate and sulphate had significant influence upon the species distributions. After all of the partial CCAs were run it was determined that the variables of pH, sodium and potassium did not have significant influence upon species distribution. They were omitted from all subsequent analyses.

Another CCA was run on 39 samples and 8 environmental variables. Extreme samples, those with extreme environmental variables and/or species assemblages (> five times influence), were identified. Sample 85 had an extreme water depth, samples 89 and 90 had missing values for bicarbonate, and sample 92 had a large population of *Stephanodiscus hantzschii* (46%). This species only occurred in four other samples, with relative percent abundance ≤ 4%. Three out of four of those samples were omitted through the data screening procedures. Samples 85, 89, 90 and 92 were removed from further analyses. Another CCA was run, and 1 variable, TDS, was identified with a high VIF value. This variable was omitted from further analyses.

V.D.2. Ordination

The final CCA was run on 35 samples, 75 species and 7 variables. Eigenvalues on the first 2 CCA axes were high (λ_1=0.382; λ_2=0.345) and significant (p_1=0.01; p_2=0.01) (Fig. V-3 & V-4). These axes explained 19 % of the cumulative variance in the diatom data, and 60.4 % of the cumulative variance in the diatom-environment relationship. A strong relationship between these diatom species, and the 7 environmental variables was evident by the high correlations between the variables and the axes (R_1=0.884; R_2=0.949).

Forward selection was run to determine which variables explained significant variation in the species data. Magnesium (26%) followed by TP (21%), lake area (16%), and calcium (12%) all explained significant proportions in diatom variance. In the CCA summary (Table V-3), and in the CCA biplots (Fig. V-3 & V-4), these variable names are written in bold. The remaining 3 variables did not explain significant proportions of the diatom species variance. The lack of significance of water depth suggests that 3.5 m was a reasonable cut off for this study.

The ordination sample scores are linear combinations of environmental variables (ter Braak, 1987). The contribution of a variable to an axis is measured by canonical coefficients. The significance of the coefficient is determined through a t-value. TP followed by calcium and water depth had significant coefficients on axis 1, while magnesium and lake area had significant coefficients on axis 2 (Table V-3). The correlation of an environmental variable to an ordination axis is determined by the intra-set correlation value (ter Braak, 1986). In some cases interpretation of relationships is best done through the use of intra-set correlation values over canonical coefficients, due to the occasional instability of canonical coefficients, and because coefficients are only comparable if the environmental variables have been standardized (ter Braak, 1986). Axis 1 was clearly a phosphorus concentration gradient, while axis 2 was a gradient of magnesium and bicarbonate concentration. Of these latter two variables on axis 2, only magnesium was identified through forward selection as significant, and only the coefficient for magnesium was significant, therefore axis 2 represented a gradient of magnesium concentration.

TP concentration increased toward the right on axis 1 and magnesium concentration increased toward the top on axis 2 (Fig. V-3 & V-4). The ordination axes separated lakes with high concentrations of TP, and low concentrations of magnesium (e.g., 8, 10, 21, 28 & 71) on the right of axis 1, from lakes with lower TP concentration and high magnesium concentration (e.g., 73, 83, 77 & 81) in the upper left corner. Lakes to the right on axis 1 had moderate to high TP concentration. In these lakes on the right that were positioned from bottom to top along axis 2 (samples 9, 22, 72, 78, 84 & 87), the concentration of magnesium ranged from low to high (3-44.6 mg/L). Lakes to the left on axis 1 had extremely low to moderate concentrations of TP (4-49 μg/L). Magnesium ranged from extremely low to very high in the lakes distributed from bottom to top along the left side of axis 2 (1-115 mg/L). Lakes in the lower left corner had very low TP (4-10 μg/L) and magnesium concentration (1–2 mg/L). The lake samples just above the x-axis had moderate concentrations of TP (6-41 μg/L) and magnesium (10-43 mg/L). Finally, the lakes in the upper left corner (73 & 83) had moderate concentrations of TP (32 & 49 μg/L, respectively), but very high concentrations of magnesium (115 & 64.5 mg/L, respectively).

Magnesium, bicarbonate and sulphate were all strongly correlated variables (correlation matrix not shown). They were the only significantly correlated variables in the final CCA ($p \leq 0.05$). Calcium and TP were statistically unrelated variables, yet the scores for the arrowhead positions were similar.

Some geographically distinct groups of lakes were distinguished on the biplot. Samples 5 to 28 represented lakes from the Birch Mountains (northeastern Alberta) (Fig. V-1). All of these lakes were positioned in the lower right corner of the biplot (Fig. V-3). These lakes from northeastern Alberta had similar chemical and physical features (Table V-2). The three lakes located on the Canadian Shield (northeast corner of Alberta; numbers 63, 4 & 66) all had very dilute chemistry, and were positioned in the lower left corner of the biplot. This is another region of the province that had lakes with very similar features (Table V-2). Many lakes from central Alberta, the southern Boreal Forest, the Aspen Parkland, and transition ecoregions were sampled (Fig. V-1). Lakes from these regions were positioned throughout the biplot, but mainly above the x-axis (Fig. V-3).

Some geographically adjacent lakes (e.g., 83 & 84; or 72 & 73) had very different values for some chemical and physical variables in addition to different species composition. In contrast, some geographically separate lakes (e.g., 73 & 83; or 72 & 84) had very similar values for some lake-chemistry variables, and similar assemblages of diatom species. For example, lakes 73 and 83, in the upper left corner, had high concentrations of TP, and the highest concentrations of magnesium of the entire data set. Both lakes also had high relative abundance of *Fragilaria brevistriata* (69) (numbers in parentheses following species name refer to species numbers in Table V-6 & Fig. V-4). This was a common species in the data set (it occurred in 25 lakes), but it was most abundant in these two lakes (82% & 58% relative abundance, respectively). This is an alkaliphilic, high nutrient tolerant species (Lowe, 1974; Beaver, 1981). The similarity of ordination scores of these 2 samples on the biplot was due to very high concentrations of magnesium and similar species assemblages.

The relationship between species and environmental variables on the ordination diagram is indicated by species scores and projection arrows representing the variables (ter Braak, 1987) (Fig. V-4). Species were positioned along the TP (axis 1), and magnesium gradients (axis 2). The final ordination scores calculated for each species represents estimated optima along all environmental trajectories included in the analysis (ter Braak, 1987). The position of the symbols on the biplot represent the final ordination scores for the species, while the symbol indicates the number of times a species occurred in the 35 lake data set. Species numbers with corresponding names are given (Table V-6). Species that preferred low concentrations of TP and magnesium were positioned in the lower left corner, while those species that preferred lakes with high concentrations of TP and magnesium were positioned in the upper right corner. Lakes with those characteristics were also positioned in the lower left, and upper right corners, respectively (Fig. V-3).

The range in species scores was smaller than the range in sample scores (Fig. V-4). There were many species (48) that occurred in less than 5 lakes. Only 7 species occurred in more than 20 lakes, and the remaining species (19) occurred in 5 to 20 different lakes in the data set. Many of the rare species (≤ 4 occurrences) were positioned in the lower left corner. Many of these species occurred in the oligotrophic (low TP concentration) lakes.

Many of the oligotrophic lakes also had low concentrations of other ions, and they had more diverse species assemblages than the eutrophic (high TP concentration) lakes.

The ordination axes separated oligotrophic, softwater (low magnesium and calcium concentration) lakes (numbers 63, 64 & 66) from eutrophic, hardwater (high magnesium and calcium concentration) lakes (numbers 28, 69 & 74) (Fig. V-3). The former lakes had species assemblages of *Achnanthes minutissima* (7), *Cyclotella radiosa* (34), *Tabellaria flocculosa v. flocculosa* strain IV *sensu* Koppen (1975) (156) and *T. flocculosa v. flocculosa* strain IIIp *sensu* Koppen (1975) (157). The eutrophic, hardwater lakes had species assemblages of *Aulacoseira granulata* (21), *Fragilaria crotonensis* (77), *Stephanodiscus niagarae* (152) and *S. parvus* (153).

Planktonic and benthic species were distributed throughout the biplot across the gradients of TP and magnesium concentration (Fig. V-4). Along the first axis, groups of species with similar scores were evident. They had similar inferred TP concentration optima. Within these groups, the species had varying scores along the second (magnesium) axis. Oligotrophic indicator species such as *Aulacoseira distans* (20), *Cyclotella hakansonniae* (31), and *C. tripartita* (36), were positioned on the far-left side of the biplot. Progressively more nutrient tolerant species were positioned towards the right on the first axis. The next groups of species with similar scores on the first axis were *Cyclotella distinguenda* (30), *C. stelligera* (35), and *Tabellaria flocculosa v. flocculosa* strain IIIp (157). The next two groups included first *C. meneghiniana* (32) and *C. radiosa* (34), and second *A. italica* (22) and *Fragilaria crotonensis* (77). These groups were positioned further to the right on the first axis, respectively. Finally, the most eutrophic indicator species, *Asterionella formosa* (17), *Aulacoseira ambigua* (19), *A. granulata* (21), *Fragilaria nanana* (82), *Stephanodiscus niagarae* (152) and *S. parvus* (153) were positioned on the right side of the biplot. *Gomphonema parvulum* (97), a periphytic species, was positioned at the high end of the TP gradient. This species is known to prefer water with higher nutrient status (Lowe, 1974). This species was rare in the data set (it occurred in two lakes) and only at a maximum relative abundance of 2% in sample 88. Within these different groups of species, estimated TP concentration optima were similar, but estimated magnesium concentration optima were different. For example, both *Aulacoseira italica* (22) and *Fragilaria crotonensis* (77) preferred mesotrophic water, but the former species preferred water with low magnesium concentration, while the latter species preferred water with high magnesium concentration. *Amphora libyca* (12) also preferred mesotrophic water, but in comparison to *Fragilaria crotonensis* (77), it preferred water with even higher magnesium concentration.

Some benthic species, for example *Fragilaria construens v. construens* (74), *F. construens v. venter* (76), and *F. pinnata* (85), had similar positions along both the TP and magnesium gradients. *Cymbella cesatii* (39) and *C. microcephala* (42) were found in oligotrophic lakes. *Navicula* cf. *mediocris* (160), *N. pupula* (121) and *N. cryptocephala* (105) had similar positions along the TP concentration axis, but were distributed from low to high, respectively, along the magnesium concentration gradient. In contrast, *N. radiosa* (122), *N.* cf. *submuralis* (162) and *N.* cf. *mediocris* (160) all preferred low magnesium concentration, but they preferred progressively higher TP concentration. *Stephanodiscus niagarae* (152) and *S. parvus* (153) were generally found in lakes with abundant phosphorus and moderate magnesium, while species of *Aulacoseira* (n=4) and *Cyclotella* (n=7) were found in lakes across the TP and magnesium concentration gradients.

V.D.3. Regression and Calibration

Phosphorus was an important variable in the data set, and is limiting in some ecosystems (Cole, 1979). Regression and calibration methods were used to estimate species TP concentration optima, and to develop an equation to infer TP concentration in a sample based upon species composition. In a CCA constrained to TP, the eigenvalue of the first axis was 0.27. This was significant ($p \leq 0.05$), as determined by Monte Carlo tests with 99 unrestricted permutations. The ratio of the first two eigenvalues in this constrained CCA was 0.58. This ordination constrained to TP was used to assess the strength of the variable in the data set (ter Braak, 1987).

A final set of 30 lakes was used in the weighted-averaging regression and calibration procedure. From the 35 lakes used in the final CCA, another 6 lakes were omitted (10, 22, 40, 69, 78 & 88) because they had high TP values (>120 µg/L). The TP concentration in Lake 89 was within the range of values for the other lakes, and so this lake was re-entered into the data set. Sample 89 was only removed initially because a measurement for bicarbonate was missing. A summary of some of the environmental variables for the 30 lakes used in the calibration were calculated (Table V-4). The summary was derived from untransformed values, but for the regression and calibration procedures the values were ln (x+1) transformed.

Thirty lakes were used in weighted averaging (WA) regression and calibration equations to derive a model to infer TP from sedimentary diatom assemblages. Untransformed and square root transformed species data were used in both simple WA and WA with inverse weighting by species tolerance (WA_{tol}). Finally, both inverse and classical deshrinking procedures were employed. In total eight different equations were derived (Table V-5). High correlation coefficients (r), low root mean squared error (RMSE) values, and lack of significant trends in the residuals were used as criteria to determined the best equation. In all trials, WA produced slightly lower correlations, but also lower RMSE values as compared to WA_{tol}. WA with square root transformations of the species data produced lower apparent RMSE values, and higher correlation coefficients than simple WA with no species transformations (Table V-5). This occurred with both inverse and classical deshrinking. Significant trends in the residual plot occurred 4 times. Significant trends occurred with inverse deshrinking, transformed and untransformed species data, and simple WA and WA_{tol} (Table V-5).

Simple WA, with square root transformation of the species data and classical deshrinking produced the best equation. By using simple WA with square root transformation of species data, higher correlations and lower error estimates were produced than in equations with no species transformations (Fig. V-5). The correlation values in both of these regression equations were significant, but when species data was square root transformed, lower RMSE values were derived. The calibration equation with transformations produced smaller deviations from the trendline than the equation without transformation. Estimation of TP optima for 71 species was calculated from this equation (Table V-6). The equation was $y = 2.533 + 0.270x$, where y and x represent the corrected and uncorrected estimates for TP (Birks *et al.*, 1990).

Lake water TP concentration versus the relative abundance of 12 common species in the calibration set was plotted (Fig. V-6). Some species, for example, *Amphora pediculus* and *Cyclotella radiosa*, although common in the data set, never occurred at more than 12% relative abundance in any lake. This was in contrast to the species *Aulacoseria granulata, Fragilaria brevistriata* and *Stephanodiscus parvus* that occurred at more than 45% relative abundance in two, two and four lakes, respectively. *F. brevistriata* was otherwise only moderately abundant (≤ 10%) in most other lakes. The estimated TP optimum would be highly weighted by the site value in the two lakes in which the species was overwhelmingly dominant.

Asterionella formosa, Aulacoseira granulata, F. crotonensis, S. niagarae and *S. parvus* occurred at similar relative abundance across the TP concentration gradient. *F. construens v. venter* also had similar abundance until about 75 µg/L when its abundance decreased. The relative abundance of *Aulacoseira ambigua* increased as TP concentration increased. For *Cyclotella radiosa* and *F. construens v. construens*, the relative abundance in a lake decreased as lake-water TP increased. The abundance of *Amphora pediculus* and *F. brevistriata* were lower in lakes with more than 40 µg TP/L, while the abundance of *F. pinnata* was lower in lakes with more than 35 µg TP/L.

V.E. Discussion

V.E.1. Data Screening

Data screening procedures are employed to remove superfluous environmental variables, and samples with unusual species assemblages and/or extreme values for one or more environmental variables (Hall & Smol, 1992).

Samples 32 and 82 were identified as outliers. Sample 32 was a dilute lake. Low dissolved phosphorus limited the planktonic community, and this allowed a benthic community, dominated by *Navicula* species, to flourish. For sample 82, the water had high concentrations of dissolved matter (TDS and ions). The diatom community was overwhelmingly dominated by *Fragilaria capucina v. mesolepta*. These two samples were extremes at opposite ends of dissolved ion gradients.

Samples 85, 89, 90, 91 & 92 were also removed due to extreme environmental values, missing environmental values, and/or unusual species assemblages. Amisk Lake (85) was an unusual lake in this data set because it is a long, narrow, and deep lake, and *Stephanodiscus niagarae* (24%) and *S. parvus* (71%) dominated the diatom assemblage. Some small species of *Stephanodiscus* often dominate in lakes with high TP concentration (Reavie *et al.*, 1995), likely due to a low silica to phosphorus ratio (Bradbury, 1988; Fritz *et al.*, 1993). A ratio of 20 between silica to phosphorus was calculated for this lake. This was low in comparison to other ratios available for this data set (not reported). These two species of *Stephanodiscus* were likely good competitors due to other factors such as deep water, large water volume, and steep basin morphometry with little illuminated sediment area, in addition to a low silica to phosphorus ratio.

Baptiste Lake (92) was overwhelmingly dominated by *S. hantzschii* (46%), with *Aulacoseira granulata* (27%) as a sub-dominant. *S. hantzschii* was rare in the data set as a whole, and it has been suggested that this species responds to cultural eutrophication (Anderson & Rippey, 1994; Bennion, 1994). TP concentrations in this lake can fluctuate up to three fold from June to August, but the TP measurement recorded in this study agreed with the average of ice-free season (June to October) measurements by Mitchell and Prepas (1990). This illustrates that an average of many measurements over a year, or one measurement of a variable for a lake do not produce a complete picture of a lake's chemistry, although in this example the average and the single measurement were equivalent. *Stephanodiscus hantzschii* has dominated the diatom assemblages in Baptiste Lake for over 4000 years (Hickman *et al.*, 1990), and the lake is currently classified as hyper-eutrophic (Mitchell & Prepas, 1990). These results confirm that this species is an indicator of eutrophic conditions, and that Baptiste Lake is an example of a naturally eutrophic lake. In addition, the dominance of this species in the surficial sediments, and in the samples from a long sediment core, indicate that the other species that may have been present when TP concentration was extreme (summer and late fall) either were not preserved, or were not diatom species.

Some of the environmental variables of the data set were also removed because measurements were incomplete for the entire data set, they did not significantly influence diatom species distributions, or unreliable canonical coefficients were derived for them. Nine environmental variables (chloride, silica, organic carbon, sodium, potassium, total dissolved solids, conductance, alkalinity and pH) were removed from the original data set for these reasons.

V.E.2. Ordination

The final CCA was run on 35 samples, 7 environmental variables and 75 species (Fig. V-3 & V-4). The eigenvalues were high and significant. The results from this ordination were comparable to those from other studies (Dixit *et al.*, 1991; Hall & Smol, 1992; Christie & Smol, 1993; Jones *et al.*, 1993; Pienitz & Smol, 1993; Bennion, 1994; Reavie *et al.*, 1995) in terms of eigenvalues, species-environment correlations, and percent variance explained by diatom species alone, and diatoms with environmental variables.

In Chapter IV, water depth was determined to be the overriding factor that influenced diatom species assemblages across lakes of all depths. Maximum depth of the lake water strongly influenced the development of algal community type. Through shallow water, light can reach a large submersed sediment area, and a benthic community may dominate (Round, 1981). In deeper water a large water volume is present, less light reaches the sediments, and a planktonic community may dominate. In addition, benthic species are likely influenced by phosphorus from sediment or host plants (Bennion, 1994). By removing lakes with a predominantly planktonic flora, an underlying influence of community type is also removed. From the large data set (n=93) of lakes used in Chapter IV, 40 deeper lakes were chosen and used in the present study. The lakes used in this study had water depth greater than 3.5 m. Two additional lakes were also added (numbers 22 and 40). They were shallow (1.3 m & 2.5 m, respectively) but had high planktonic populations (42% and 84%, respectively). Water samples indicated that these 2 lakes were eutrophic (TP concentration > 85 µg/L). Direct ordination of the larger data set revealed that these two lakes were similar to lakes with maximum water depth greater than 3.5 m, both in species assemblages and water chemistry (Chapter IV). Site 22 was positioned close to sites 5, 9 and 11 on the biplot (Fig. V-3). The diatom assemblage in the sample from site 22 was similar, but the TP concentration was much higher in site 22 than in the other three lakes. In comparison, site 40 was positioned close to sites 69, 74, 86 and 93. The species assemblages were also similar in this group, but the TP concentration at site 40 was within the range of values found in those adjacent sites. It is known that high nutrients stimulate phytoplankton communities (Schindler, 1985). In these two cases a planktonic community was supported. It dominated irrespective of lake water depth, and the benthic community was limited due to shading of the substrate.

Concentration of TP and magnesium were the two most important variables in this data set, and two variables that significantly influenced species distributions. Axes 1 and 2 represented gradients of TP and magnesium concentration, respectively (Fig. V-3 & 4). The significance of a nutrient gradient in this data set was not unexpected because total phytoplankton biomass is related to the concentration of TP (Zhang & Prepas, 1996). Phosphorus is a limiting nutrient in most freshwater ecosystems (Cole, 1979). Lakes can be classified as oligotrophic, mesotrophic or eutrophic based upon the TP concentration in a sample (Forsberg & Ryding, 1980). Other workers have also used TP alone or in combination with other variables to define lake trophic status (e.g., Agbeti & Dickman, 1989; Prepas, 1990; Yang & Dickman, 1993). Species assemblages of the phytoplankton change when excess nutrients are added to the water (Schindler, 1985), but this is in addition to species succession that occurs naturally over the growing season (Round, 1981). The surficial sediment samples analyzed in this study were assumed to contain a mixture of the species assemblages over the previous few seasons (Dixit *et al.*, 1995). It was therefore assumed that species succession was accounted for in these surficial sediment samples.

Some studies have revealed water depth as the most important variable influencing species distributions (e.g., Hall & Smol, 1992; Bennion, 1994; Chapter IV). In some studies only variables related to trophic status (i.e. TP, TN, chlorophyll *a*, and secchi depth) were identified as the primary variables influencing diatom species distributions (Agbeti, 1992; Christie & Smol, 1993; Fritz *et al.*, 1993; Bennion, 1994). In a data set of British Columbia lakes, water depth was more important than the concentration of TP in influencing diatom species assemblages (Hall & Smol, 1992). As more eutrophic lakes were added to the data set, water depth decreased in importance, while TP concentration increased in importance (Reavie *et al.*, 1995). Abundant nutrients in water can therefore strongly influence planktonic species dominance, and planktonic species composition.

In some studies (Hall & Smol, 1992; Reavie *et al.*, 1995) other water chemistry variables such as calcium concentration and conductance, in addition to TP and water depth, significantly influenced diatom species distributions. In this study, other important variables were calcium concentration and area of the lake. Calcium concentration in this study was comparable to calcium concentration in the British Columbia lakes (Hall & Smol, 1992; Reavie *et al.*, 1995). The relationship between diatom species, calcium and TP concentration was not investigated in the previous studies. Calcium is one of the ions used to determine lake water salinity, but the independent influence of calcium was not investigated by others (Cumming & Smol, 1993). Calcium and magnesium ions are also components of water hardness (Wetzel, 1975). It was suggested that water hardness might suppress diatom phytoplankton (Chapter IV). In both the previous analysis, and this present data set, magnesium concentration was an important variable. There is clearly an association between magnesium concentration and the distribution of diatom species in Alberta lakes. This could be explored further by experimentally manipulating magnesium concentration and observing the effect upon species assemblages.

There was some geographical grouping of lakes on the ordination biplot (Fig. V-1 & V-3). Lakes from northeastern Alberta were positioned in the lower right corner, and lakes from the extreme northeast were positioned in the lower left corner. Lakes from central Alberta were distributed throughout the biplot, but mostly above the x-axis. Geography influenced the chemical composition of many of these lakes. Fertile prairie and parkland soils cover much of central to southern Alberta (Strong & Leggat, 1981). These soils easily release phosphorus. In central Alberta there is much agricultural and cottage development in the catchments of the lakes. Consequently the lakes in this area receive phosphorus inputs. In northern boreal Alberta, acid forest soils and organic soils cover much of the area, and they release very little phosphorus into the lakes (Prepas, 1990; Halsey *et al.*, 1997). Forestry and gas exploration are currently the dominant disturbance types in northern Alberta (Bailey, 1989; Forestry, Lands and Wildlife, 1992; Alberta-Pacific, 1994). These activities do not directly supply nutrients to the lake, but depending upon the extent of disturbance in a catchment, erosion and surface water flow may increase which may indirectly increase nutrient inputs. Anthropogenic disturbances may help to explain some of the grouping of the samples in the ordination. Samples above the x-axis (except number 40) are located in areas of agricultural and cottage development, and samples below the x-axis are located in Boreal regions with different types of land use. Perhaps there is an underlying gradient on axis 2 reflecting they type of anthropogenic disturbance to a lake. The influence of different types of human disturbances upon a lake could be investigated by analyzing short sediment cores from multiple lakes (e.g., Dixit *et al.*, 1992). Current and past (*ca.* 1800 to 1850) diatom assemblages could be compared to determine how impacts have affected various lakes.

V.E.3. Regression and Calibration

The reliability of a calibration equation depends upon the relationship between the species and the environmental variable. In a CCA constrained to one variable, a ratio of the first 2 eigenvalues above 1 indicates a strong relationship between the species and the variable (Fritz *et al.*, 1993). The ratio of the first two eigenvalues in a CCA constrained to TP was 0.58. Results from these analyses were comparable to other studies that focussed upon the relationship between TP concentration and species assemblages (Hall & Smol, 1992; Bennion, 1994; Reavie *et al.*, 1995). Diatom species assemblages in these Alberta lakes were significantly influenced by TP concentration of the water. The fact that the eigenvalue ratio was much lower than the one obtained by Fritz *et al.* (1993) indicated that other variables also played a role in influencing diatom species distributions. In these lakes, magnesium concentration had a significant influence upon species assemblages, while in some British Columbia lakes, conductivity had a significant influence upon species distributions (Reavie *et al.*, 1995). The paucity of annual measurements available for each lake in the data set may also produce lower correlations and less significant relationships (Reavie *et al.*, 1995). Ideally there should be multiple measurements of each environmental variable for each lake over the entire growing season, although this is not always possible. The sediment sample contains a matrix of species that have occurred in the lake over the previous few growing seasons. Therefore, an ideal environmental data set would also contain an average of values for the various variables obtained from many readings over a few seasons. Anderson *et al.* (1993) showed a better correlation between mean observed yearly TP and diatom inferred TP than between seasonal (December measurements) observed TP and diatom inferred TP.

The equation to infer TP concentration from sedimentary diatom assemblages was derived from 30 lakes. In total eight different equations were derived (Table V-5). It was determined that simple WA, with classical deshrinking, and square-root transformation of species data produced the best equation. Transforming the species data improved the correlation between observed and inferred TP (Reavie *et al.*, 1995).

The predictive ability (Wilson *et al.*, 1996) was better when species data was transformed as compared to when it was not. A transformation of species data reduces the range in the data in the same way that the range in the environmental data was reduced by natural log transformation. This produces consistent estimates of species TP optima and consistent estimates of site TP values. It was found in this study and by others (Cumming *et al.*, 1994; Reavie *et al.*, 1995) that by transforming species data, correlations improved greatly, and RMSE values decreased greatly. The correlations between observed and diatom inferred TP were high and significant, and were comparable to other studies that examined diatom and phosphorus/nutrient relationships (Hall & Smol, 1992; Fritz *et al.*, 1993; Bennion, 1994; Reavie *et al.*, 1995). The RMSE values were also comparable to these studies.

Techniques of deriving inference equations are always being improved upon. In the 1980's, calibration sets were collected, but equations were derived using multiple linear regression (e.g., Charles, 1985; Dixit, 1986; Agbeti & Dickman, 1989; Whitmore, 1989). ter Braak and van Dam (1989) compared various techniques for deriving equations, and determined that the best results were produced from models that assumed a unimodal response between species and environmental variables. Some of the first unimodal models were derived for pH (e.g., Birks *et al.*, 1990; Charles *et al.*, 1990; Dixit *et al.*, 1991; Cumming *et al.*, 1992). Since then, inference equations based on unimodal techniques have been derived for other variables such as TP (e.g., Agbeti, 1992; Anderson *et al.*, 1993; Fritz *et al.*, 1993; Bennion, 1994), nitrogen (Christie & Smol, 1993), salinity (e.g., Cumming & Smol, 1993; Wilson *et al.*, 1996) and dissolved organic carbon (Pienitz & Smol, 1993). The correlations from nutrient-diatom relationship studies are always lower than the correlations obtained from pH-diatom studies (Hall & Smol, 1992) because of the effect of pH upon cell physiology (Charles, 1985). In the presence of excess phosphorus, most algae will store extra phosphorus in their cells for later use (Round, 1981). The relationship between diatoms and TP can be variable, and this could also account for the lower correlation values obtained in these studies as compared to diatom-acidification studies.

Many North American lakes are oligotrophic to mesotrophic, while those from England and Ireland are eutrophic, presumably due to high land use (Reavie *et al.*, 1995). This original data set of Alberta lakes contained some very eutrophic lakes, but these were rare. There are additional lakes in Alberta with high TP concentration (Mitchell & Prepas, 1990) that could be included to increase the range in TP concentration in this data set. Ideally more lakes would be added to this data set to smooth the distribution of samples across this gradient.

The response of 12 species to the TP concentration gradient was illustrated (Fig. V-6). Some species appeared to have a unimodal response, some had a linear response (higher or lower abundance in lakes with higher TP), while some had no response (similar abundance in lakes at varying TP concentration). The relationship between species abundance and an environmental gradient has been observed to be unimodal (ter Braak & van Dam, 1989). The length of the gradient plays an important part in this relationship. If a gradient is too short then the "true" optimum for a species along an environmental gradient can not be determined. The presence or absence of a species in a lake is determined by more than just one variable. Other abiotic and biotic factors influence the presence and abundance of a species. For example, there may be preferential selection for planktonic diatoms by some zooplankton grazers (Miskimmin, 1995). Perhaps with the addition of more lakes within this TP range, more species would show a unimodal response.

The relative abundance of *Aulacoseira ambigua* tended to be higher in lakes with higher levels of TP. The TP gradient was probably too short since a much higher TP optimum was estimated from a set of eutrophic ponds (Bennion, 1994). *Fragilaria brevistriata* was typically low (≤ 10%) in most lakes. In two lakes it occurred at more than 50% relative abundance, and as a result, estimated TP optimum for *F. brevistriata* was highly weighted by the TP concentration value in these two lakes (32 and 49 µg TP/L). Environmental parameters in these two lakes were ideal for this species, or this species was a better competitor than all other species in these two lakes.

The abundance of some species (e.g. *Cyclotella radiosa*) decreased over the TP gradient, while other species (e.g. *Amphora pediculus*) had a lower abundance in lakes with a phosphorus concentration greater than 40 µg/L.

The optimum TP concentration for 71 diatom species was estimated (Table V-6). The range in TP estimates of all species was larger than the range in estimates reported by Hall & Smol (1992) and Fritz *et al* (1993), and much lower than those reported by Bennion (1994). Actual estimates of species optimum TP did vary between this study and that of Reavie *et al.* (1995), even though the range in lake water TP concentration, and the range of all species estimates was similar. For example, optima derived for *Stephanodiscus niagarae* were 46.9 and 19.3 µg/L from this study and the one by Reavie *et al.* (1995), respectively. Even though the range in TP was similar, 25% of the lakes in this study were eutrophic (TP > 50 µg/L), while only 5% of the lakes in the latter study were eutrophic. Since many of the Alberta lakes have higher concentration of TP than the British Columbia lakes, estimated species optima from this calibration set should be higher. In addition, for a set of eutrophic ponds in England, (mean lake water TP concentration was 125 µg/L) (Bennion, 1994), estimates of species optima were higher than those obtained in this study. Thus, estimates of species optima are dependent upon the range in TP concentration in the calibration lakes, the distribution of lakes along the TP gradient, and the normal distribution of species abundance across the TP gradient.

Variations in estimates between data sets may be due simply to lake water TP concentration values, to dynamic physiological responses of species to unique lake conditions, or to using only a single measurement. Biological and chemical factors of a lake can have an effect upon species physiology (Dixit *et al.*, 1992). Responses to biological and chemical stresses may be observed as variations in abundance within and between lakes or as decreased production in cellular components. Experimental manipulation may help to determine effects on individual species physiology. Until further studies can explore this possibility, it is suggested that species optimum TP varies between the lakes from different regions.

The calibration model derived in this study is the first to be based on sedimentary diatom assemblages from Alberta lakes. The formula can be applied to estimate down core TP concentration values from the diatom assemblages in a lake sediment core. In these Alberta lakes, the concentration of magnesium and calcium in the water column was also important in influencing diatom species distributions. These variables were not important in some other calibration sets that focussed upon diatom-TP relationships. These other variables may affect the relationship between diatom species and TP, and in a sense make the relationship unique for regional lake sets. This underlying relationship between diatoms and TP concentration should be similar in modern and fossil diatom assemblages in many Alberta lakes. Thus, the formula to estimate TP concentration should only be applied to diatom assemblages from Alberta lakes.

V.F. Conclusions

This study originated from a larger study analyzing diatom assemblages in Alberta lakes. A subset of lakes was chosen to determine relationships between diatom species and environment in deeper lakes. In these lakes the concentration of TP and magnesium were the most important variables that significantly influenced diatom species distributions. Species were distributed along gradients of TP and magnesium concentration. Some species clearly preferred oligotrophic versus eutrophic water, while some preferred hard versus soft water. *Cyclotella* species were typical of oligotrophic, soft water lakes, while *Stephanodiscus* species were typical of eutrophic, moderately hard water lakes. *Amphora* species were typical of hard water, mesotrophic lakes, while *Navicula* species were typical of soft water, oligotrophic to mesotrophic lakes.

Statistical results from this calibration model for TP were similar to results from other calibration models. Phosphorus is a required nutrient, and the concentration of TP is statistically related to diatom species distributions across lakes, and diatom species assemblages in one lake. The analysis of environmental variables and diatom assemblages in these lakes also revealed that magnesium and calcium concentration significantly influenced species distributions. The underlying influence of magnesium and calcium makes the relationship between diatoms and TP concentration in Alberta lakes unique. The application of TP concentration models, developed from lakes in other regions, to the diatom assemblages in Alberta lakes would not provide as accurate results as those obtained from the application of this model to diatom assemblages in Alberta lakes. Many Alberta lakes are mesotrophic. Land use, vegetation cover, and geology influence lake-chemistry. These were not accounted for in this study, or any of the other studies, but they are underlying factors that may influence the relationship between species and environment. This calibration model for TP should only be applied to other Alberta lakes. This model may be of use to lake managers and other modelers when assessing lake nutrient budgets.

V.G. References

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Table V-1. Summary of data from 6 climate stations in Alberta (Atmospheric Environment Service, 1993). Locations of stations indicated on Figure V-1.

Station	Latitude (°N)	Longitude (°W)	Annual Mean Temperature (°C)	Total Precipitation (mm)	No. Days Maximum Temperature more than 0 °C	Total July Precipitation (mm)	Daily Mean July Temperature (°C)
(A) Red Deer	52° 11^{1}	113° 54^{1}	2.3	470.2	274	87.9	15.8
(B) Edmonton	53° 18^{1}	113° 35^{1}	2.1	465.8	269	101.0	16.0
(C) Ft. McMurray	56° 39^{1}	111° 13^{1}	0.2	464.7	245	79.1	16.6
(D) Grand Prairie	55° 11^{1}	118° 53^{1}	1.6	450.2	266	67.9	16.0
(E) Buffalo	57° 57^{1}	116° 13^{1}				106.8	14.4
(F) Whitesand	59° 26^{1}	114° 54^{1}				70.3	12.5

Table V-2. List of the 42 lakes used in this study with geographical position and values for selected lake variables (• indicates lake omitted from final ordination, •• indicates lake not used to generate TP inference model)

Lake Number	Lake Name	Latitude (°N)	Longitude (°W)	Depth (m)	Area (km²)	TP (μg l⁻¹)	Magnesium (mg l⁻¹)	Calcium (mg l⁻¹)	Legend
5	L18	57° 26'	112° 37'	27.00	43.39	18.00	1.50	6.00	
6	L19	57° 30'	112° 30'	10.50	7.25	36.00	4.00	16.00	
7	L20	57° 32'	112° 29'	12.50	17.48	33.00	4.00	17.00	
8	L21	57° 36'	112° 36'	13.00	17.17	65.00	3.50	11.00	
9	L22	57° 42'	112° 22'	16.00	14.58	28.00	4.00	14.00	
10	L24	57° 47'	112° 08'	3.50	8.40	210.00	4.00	12.00	••
11	L25	57° 24'	112° 56'	9.40	16.76	42.00	1.00	3.00	
21	L55	57° 13'	113° 02'	5.80	2.65	53.00	6.00	22.00	
22	L56	57° 12'	113° 03'	1.30	0.91	85.00	3.00	11.00	••
28	L62	57° 33'	112° 17'	6.00	1.48	83.00	8.00	27.00	
30	L64	58° 08'	110° 47'	4.70	4.40	18.00	3.00	12.00	
32	L67	58° 03'	110° 23'	3.60	1.07	9.00	3.00	5.00	•,••
40	L76	59° 57'	116° 32'	2.50	4.77	125.00	12.00	25.00	••
61	L104	54° 15'	119° 45'	11.00	0.54	12.00	10.00	34.00	
63	L106	59° 42'	110° 21'	8.00	1.02	8.00	2.00	7.00	
64	L107	59° 43'	110° 02'	14.10	2.72	4.00	1.00	6.00	
66	L109	59° 07'	110° 49'	5.40	3.15	10.00	2.00	6.00	
69	Steele	54° 39'	113° 46'	6.10	6.61	154.70	12.80	30.20	••
70	Mcleod	54° 18'	115° 39'	10.70	3.73	22.10	9.50	38.80	
71	Long	54° 26'	112° 45'	28.00	1.62	62.50	17.80	22.30	
72	Moose	54° 14'	110° 55'	19.80	40.80	39.00	44.60	22.90	
73	Muriel	54° 08'	110° 41'	10.70	64.10	32.00	115.00	7.00	
74	Tucker	54° 32'	110° 36'	7.50	6.65	49.00	34.00	16.00	
75	Bonnie	54° 09'	111° 52'	6.10	3.77	41.00	43.00	31.00	
76	Buck	53° 00'	114° 45'	12.20	25.40	61.00	6.00	23.30	
77	Crimson	52° 27'	115° 02'	9.10	2.32	17.40	18.00	21.30	
78	Sandy	53° 47'	114° 02'	4.40	11.40	330.00	7.80	6.30	••
79	Wabamun	53° 33'	114° 36'	11.00	81.80	36.30	14.90	22.60	
80	Pigeon	53° 01'	114° 02'	9.10	96.70	33.00	11.60	26.00	
81	Dillberry	52° 35'	110° 00'	10.70	0.80	16.80	27.30	22.30	
82	Buffalo	52° 28'	112° 54'	6.50	93.50	79.00	85.00	5.00	•,••
83	Gull	52° 34'	114° 00'	8.00	80.60	49.00	64.50	12.30	
84	Sylvan	52° 18'	114° 06'	18.30	42.80	20.00	36.00	17.60	
85	Amisk	54° 35'	112° 37'	60.00	2.82	33.10	18.21	32.52	•,••

Table V-2. Continued

86	Coal	53° 08^{1}	113° 21^{1}	5.50	10.90	72.90	12.00		
87	Sturgeon	55° 06^{1}	117° 32^{1}	9.50	49.10	62.30	5.50	21.30	
88	Moonshine	55° 53^{1}	119° 13^{1}	3.50	0.28	209.00	38.25	54.25	••
89	Crooked	54° 55^{1}	113° 33^{1}	8.50	1.09	65.00	13.88	33.20	•
90	Jenkins	54° 55^{1}	113° 36^{1}	15.00	1.46	36.90	12.72	30.00	•,••
91	Lofty	54° 43^{1}	112° 28^{1}	5.00	0.67	150.00			•,••
92	Baptiste	54° 45^{1}	113° 33^{1}	27.50	9.81	47.20	12.15	31.80	•,••
93	Pine	52° 04^{1}	113° 27^{1}	12.20	3.89	87.00	24.50	26.40	
	Minimum			1.30	0.30	4.00	1.00	3.00	
	Maximum			60.00	96.70	330.00	115.00	54.30	
	Mean			11.41	18.82	62.98	18.46	19.71	
	Median			9.25	5.69	41.50	11.60	21.30	
	SD			9.98	27.38	64.72	23.70	11.32	

Table V-3. Results of the final Canonical Correspondence Analysis performed on 35 lakes. Variable names in bold were identified through forward selection to explain significant species variation (* indicates significant at $p < 0.05$).

			t-values of		Intraset	
Environmental	Canonical	Coefficients	Canonical	Coefficients	Correlations	
Variables	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2
Depth	0.42	-0.15	*3.29	-1.79	-0.09	0.03
Area	-0.18	0.37	-1.42	*4.61	-0.17	0.53
Calcium	0.59	-0.06	*4.47	-0.73	0.57	0.33
Magnesium	-0.38	0.55	-1.29	*2.96	-0.04	0.90
Bicarbonate	-0.26	0.27	-0.91	1.49	0.06	0.90
Sulphate	0.18	0.07	1.16	0.66	0.21	0.75
TP	0.88	0.10	*6.67	1.26	0.72	0.38

Table V-4. Summary of selected environmental variables for the 30 lakes used to derive the model to infer TP concentration. For the model the TP concentration values were ln(x+1) transformed.

Environmental Variable	Units	Minimum	Maximum	Mean	Median	Standard Deviation
Depth	m	4.70	28.00	11.34	10.60	5.70
Area	km^2	0.54	96.70	21.62	6.95	27.83
TP	$\mu g\ l^{-1}$	4.00	87.00	39.21	36.15	22.92
Magnesium	$mg\ l^{-1}$	1.00	115.00	18.27	9.75	24.05
Calcium	$mg\ l^{-1}$	3.00	38.80	18.80	21.30	9.40

Table V-5. Results used to determine the best predictive model infering Total Phosphorus (TP) from sedimentary diatom assemblages. Results of transformations, deshrinking types and calibration methods are shown. The best model was determined by high correlations (r), low RMSE and insignificant trend ($p > 0.05$) in the residuals.

Transformation	Deshrinking Type	Calibration Method	r	$RMSE_{boot}$	Significant Residual Trend
None	Inverse	WA	0.842	0.550	yes
None	Inverse	WA_{tol}	0.892	0.593	yes
None	Classical	WA	0.842	0.552	no
None	Classical	WA_{tol}	0.892	0.615	no
Square Root	Inverse	WA	0.894	0.481	yes
Square Root	Inverse	WA_{tol}	0.900	0.583	yes
Square Root	Classical	WA	0.894	0.454	no
Square Root	Classical	WA_{tol}	0.900	0.603	no

Table V-6. Species names (and corresponding numbers) used in Canonical Correspondence Analysis and the weighted-averaging regression and calibration TP inference model. Species are listed by estimated TP optimum. Also given are total number of occurrences and maximum relative percent abundance in the 30 calibration lakes.

Number	Species Name and authority	TP µg l^{-1}	No. Occur.	Max. Abun.
14	*Anomoeoneis serians* (Brébisson) Cleve	4.00	1	1
41	*Cymbella gracilis* (Ehrenberg) Kützing	4.00	1	1
115	*Navicula laevissima* Kützing	4.00	1	1
36	*Cyclotella tripartita* Håkansson	4.63	2	16
31	*C. hakanssoniae* Wendker	5.23	2	11
6	*Achnanthes linearis* (W. Smith) Grunow	5.72	2	1
156	*Tabellaria flocculosa* (Roth) Kützing strain IV sensu Koppen	6.43	2	2
44	*Cymbella ventricosa* Kützing	8.03	1	1
87	*Fragilaria vaucheriae* (Kützing) Petersen	8.03	1	1
119	*Navicula pseudoscutiformis* Hustedt	8.03	1	1
133	*Nitzschii fonticola* Grunow	8.33	3	2
88	*Fragilaria virescens* Ralfs	9.40	2	6
39	*Cymbella cesatii* (Rabenhorst) Grunow	9.53	2	4
8	*Achnanthes peragalli* Brun & Heribaud	10.02	1	1
23	*Aulacoseira lirata* (Ehrenberg) Ross	10.02	1	1
109	*Navicula halophila* (Grunow) Cleve	10.02	1	1
111	*N. jaernefeltii* Hustedt	10.02	1	3
146	*Pinnularia viridis* (Nitzsch) Ehrenberg	10.02	1	1
42	*Cymbella microcephala* Grunow	10.12	5	4
148	*Stauroneis anceps* Ehrenberg	10.94	2	1
16	*Anomoeoneis vitrea* (Grunow) Ross	11.68	2	1
53	*Epithemia zebra* (Ehrenberg) Kützing	11.94	1	1
97	*Gomphonema parvulum (*Kützing) Kützing	11.94	1	1
147	*Rhopalodia gibba* (Ehrenberg) O.Müller	11.94	1	1
7	*Achnanthes minutissima* Kützing	12.54	7	2
122	*Navicula radiosa* Kützing	13.01	3	1
20	*Aulacoseira distans* (Ehrenberg) Simonsen	13.59	2	11
9	*Achnanthes suchlandtii* Hustedt	14.10	4	3
121	*Navicula pupula* Kützing	15.69	4	1
28	*Cocconeis neodiminuta* Krammer	16.81	1	1
91	*Gomphonema angustissima* Agardh	16.81	1	3
120	*Navicula pseudoventralis* Hustedt	16.81	1	1
105	*N. cryptotenella* Lange-Bertalot	17.17	2	7
30	*Cyclotella distinguenda* Hustedt	17.65	4	26
27	*Cocconeis disculus* (Schumann) Cleve	18.20	3	2
157	*Tabellaria flocculosa* (Roth) Kützing strain IIIp sensu Koppen	19.57	9	21
81	*Fragilaria leptostauron* v. *martyi* (Heribaud) Lange-Bertalot	19.99	10	9
33	*Cyclotella pseudostelligera* Hustedt	20.05	8	29
34	*C. radiosa* (Grunow) Lemmermann	20.61	12	12

Table V-6. Continued.

2	*Achanthes exigua* Grunow	20.76	3	2
35	*Cyclotella stelligera* Cleve & Grunow	21.47	9	19
74	*Fragilaria construens* v. *construens* (Ehrenberg) Grunow	23.26	19	23
4	*Achnanthes lanceolata* (Brébisson) Grunow	25.05	12	5
32	*Cyclotella meneghiniana* Kützing	25.66	2	6
137	*Nitzschii paleacea* Grunow	26.80	2	3
76	*Fragilaria construens* v. *venter* (Ehrenberg) Hustedt	26.99	21	22
85	*Fragilaria pinnata* Ehrenberg	28.49	25	30
162	*Navicula* cf. *submuralis* Hustedt	30.06	3	3
12	*Amphora libyca* Ehrenberg	30.69	8	4
69	*Fragilaria brevistriata* Grunow	32.02	22	82
136	*Nitzschii palea* (Kützing) W.Smith	33.12	1	2
160	*Navicula* cf. *mediocris* Krasske	34.34	2	1
1	*Achnanthes conspicua* Mayer	35.13	2	1
132	*Nitzschii amphibia* Grunow	35.71	3	1
13	*Amphora pediculus* (Kützing) Grunow	35.82	17	9
123	*Navicula recens* (Lange-Bertalot) Lange-Bertalot	35.97	1	1
125	*N. seminulum* Grunow	35.97	1	2
17	*Asterionella formosa* Hassall	37.05	18	16
22	*Aulacoseira italica* (Ehrenberg) Simonsen	39.33	4	23
70	*Fragilaria capucina* Desmaziérs	39.33	11	22
77	*F. crotonensis* Kitton	39.69	16	30
96	*Gomphnema minutum* (Agardh) Agardh	40.69	4	2
82	*Fragilaria nanana* Lange-Bertalot	41.22	3	13
29	*Cocconeis placentula* Ehrenberg	41.99	6	2
153	*Stephanodiscus parvus* Stoermer & Håkansson	42.64	22	59
21	*Aulacoseira granulata* (Ehrenberg) Simonsen	42.90	14	55
19	*A. ambigua* (Grunow) Simonsen	43.39	16	31
152	*Stephanodiscus niagarae* Ehrenberg	47.86	22	41
151	*S. hantzschii* Grunow	50.94	2	4
78	*Fragilaria elliptica* Schumann	82.93	1	1
71	*F. capucina* v. *mesolepta* (Rabenhorst) Rabenhorst	87.23	1	3

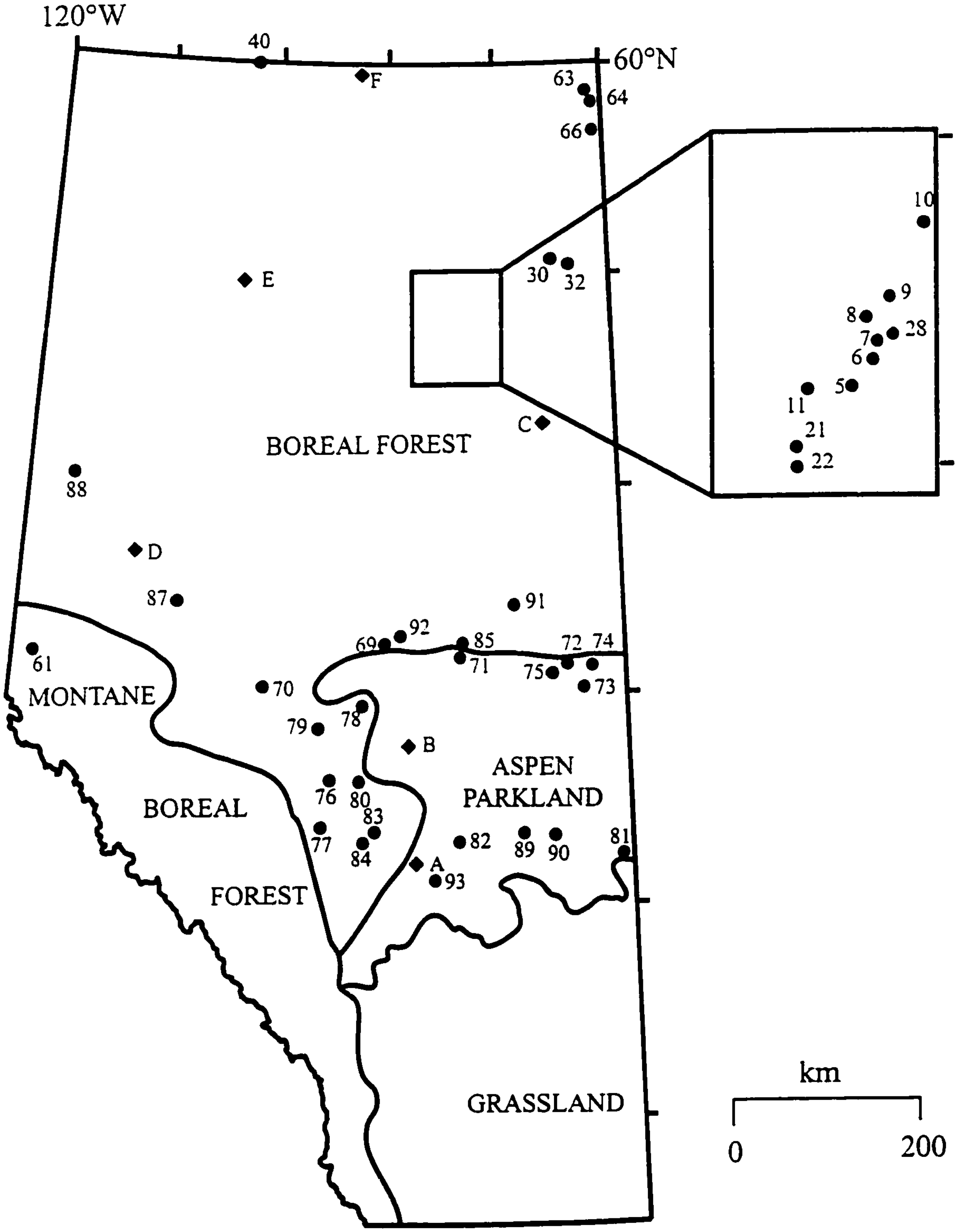


Figure V-1. Map of Alberta indicating the location of the 42 lakes (●) and 6 climate stations (◆).

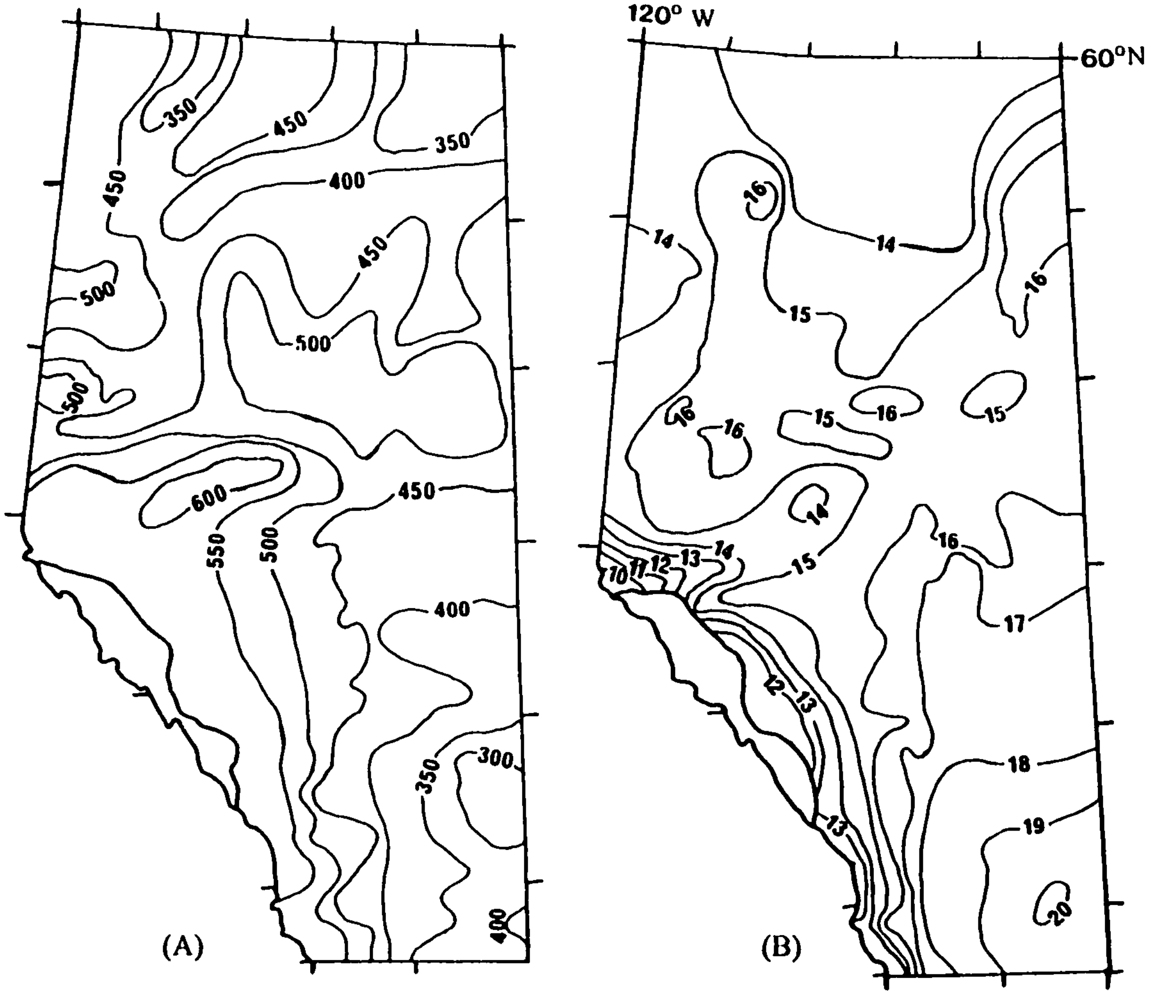


Figure V-2. General climate of Alberta as summarized by (A) total annual precipitation (mm) and (B) mean July temperature (degree C). Modified from Atlas of Alberta (1984).

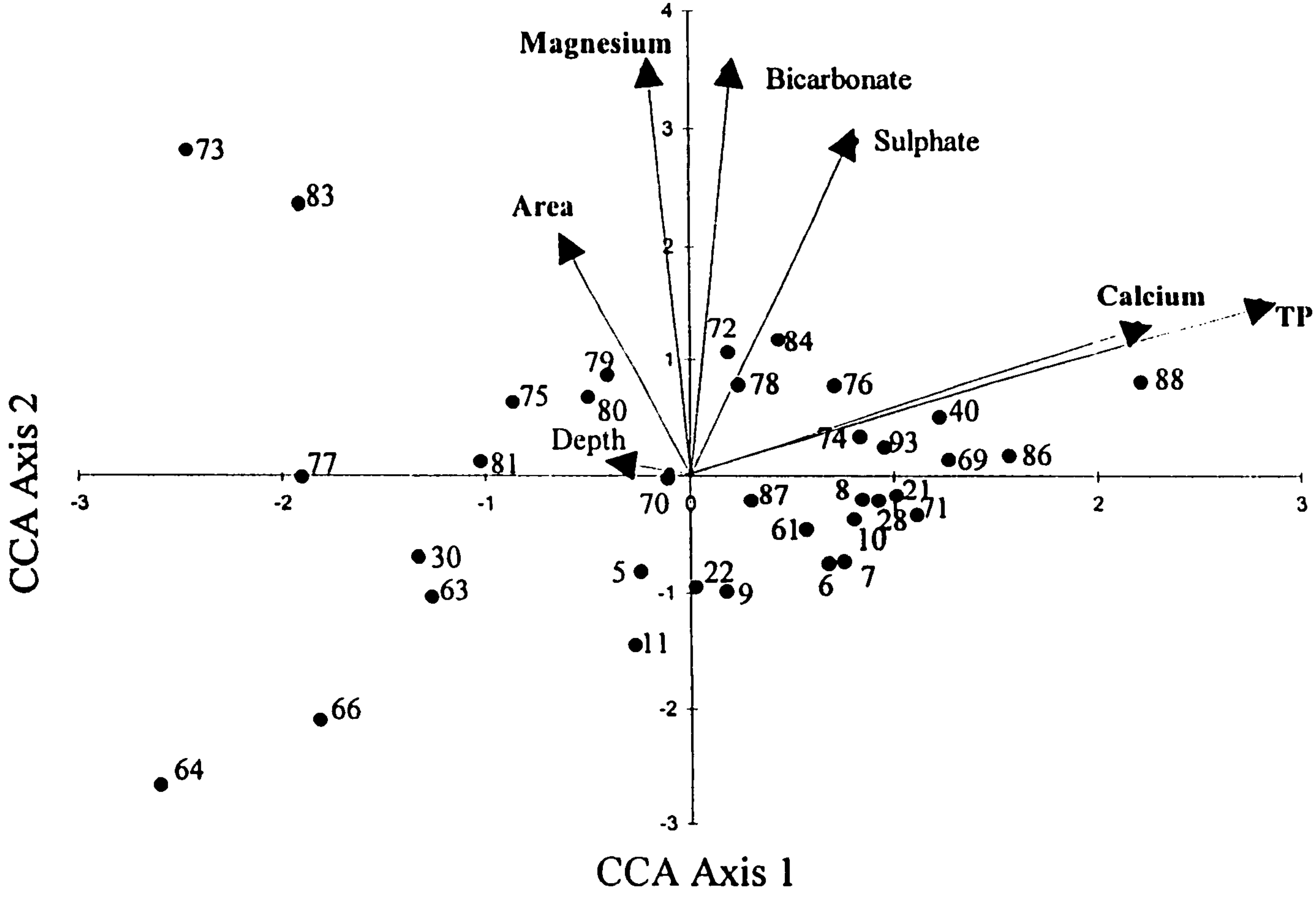


Figure V-3. Results of the final Canonical Correspondence Analysis (CCA) showing scores of 35 lakes and trajectory arrows of 7 environmental variables. Scores of environmental arrows were magnified 10-fold.

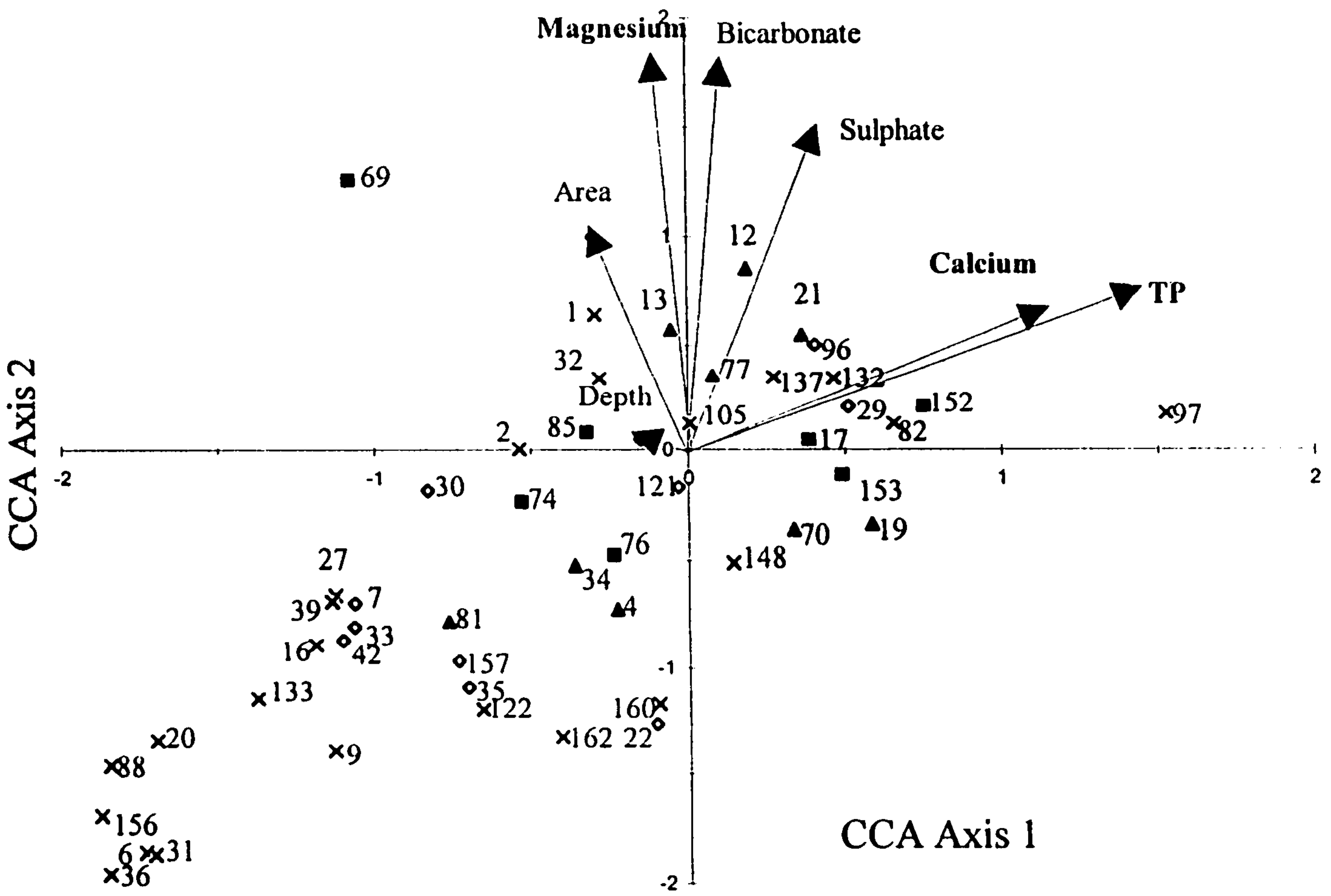
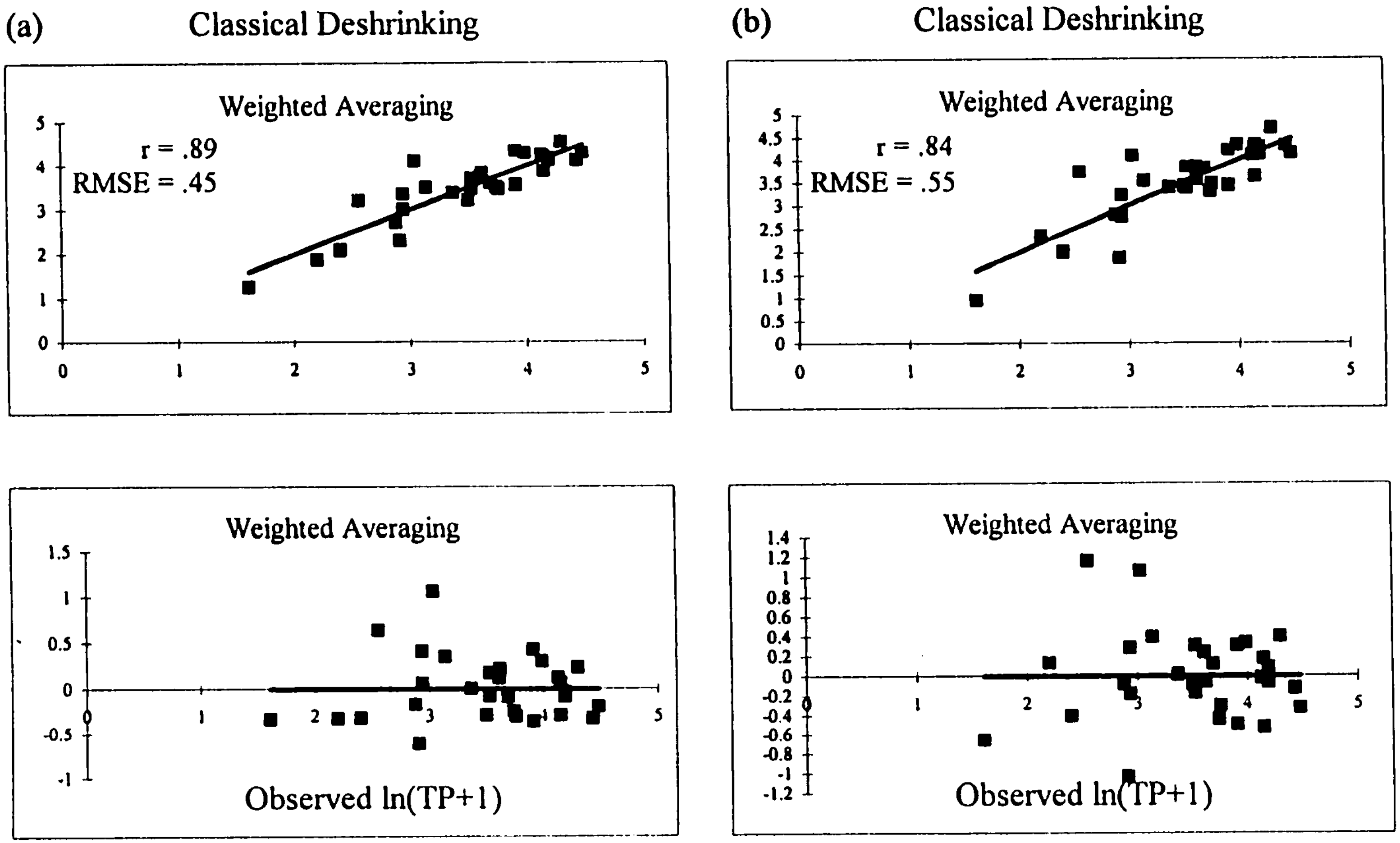


Figure V-4. Final Canonical Correspondence Analysis (CCA) results showing scores of 49 diatom species (> 1 occurrence) and trajectory arrows of 7 environmental variables. Scores of environmental arrows were magnified 5-fold. Symbols indicate number of occurrences in 35 lakes [(x)2 to 4 lakes, (◇)5 to 10 lakes, (▲)11 to 20 lakes, (■)> 20 Lakes].



Square Root Transformation of Species

No Species Transformation

Fig. V-5. Plots of observed vs inferred TP and observed vs (inferred - observed) TP. Comparison of the effect of (a) square root transformation of species data and (b) no transformation of species data. Both versions were developed by weighted averaging regression and calibration with classical deshrinking.

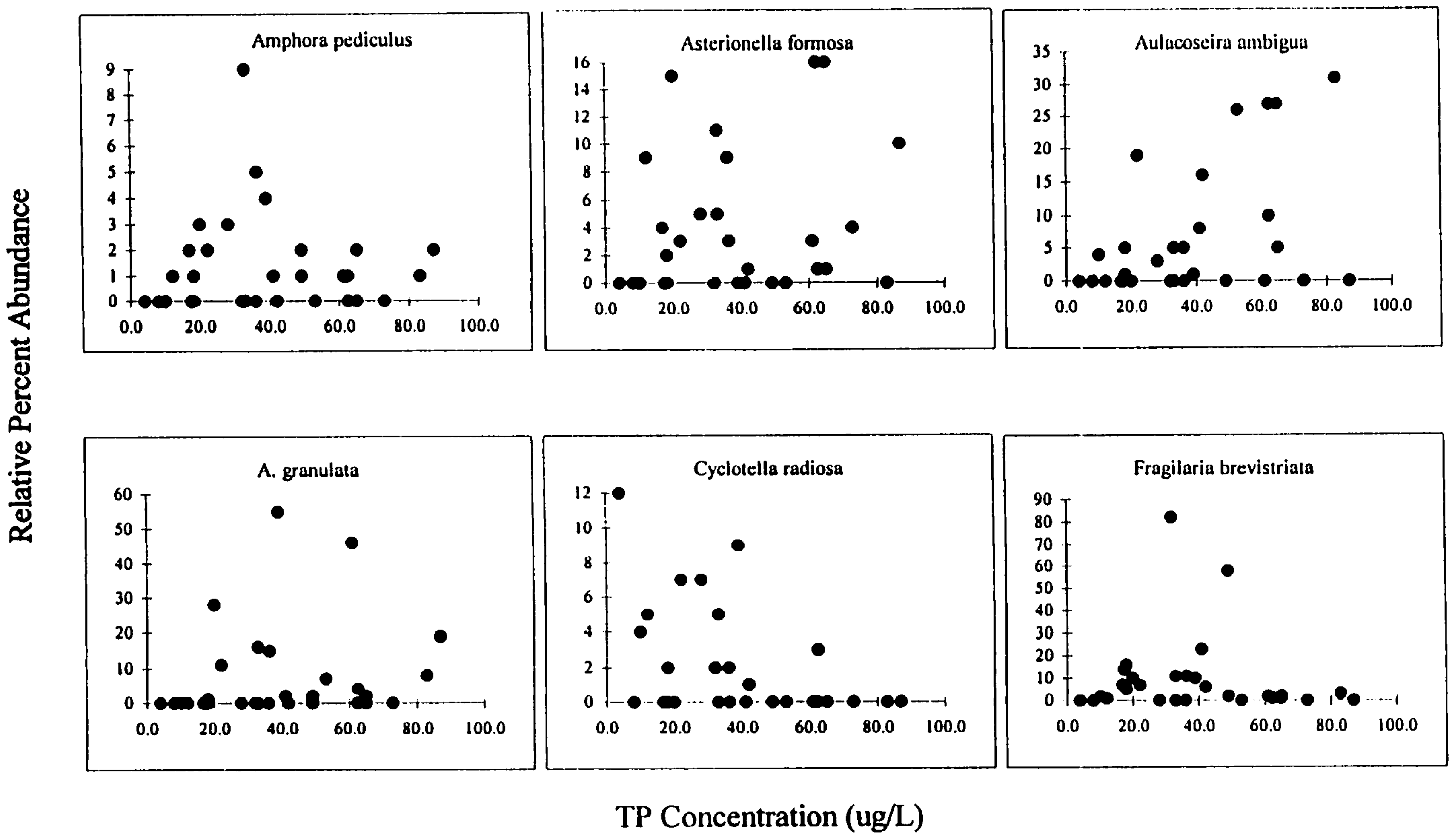


Fig. V-6. Relative percent abundance of the 12 most common diatom species in 30 calibration lakes across a total phosphorus (TP) concentration gradient.

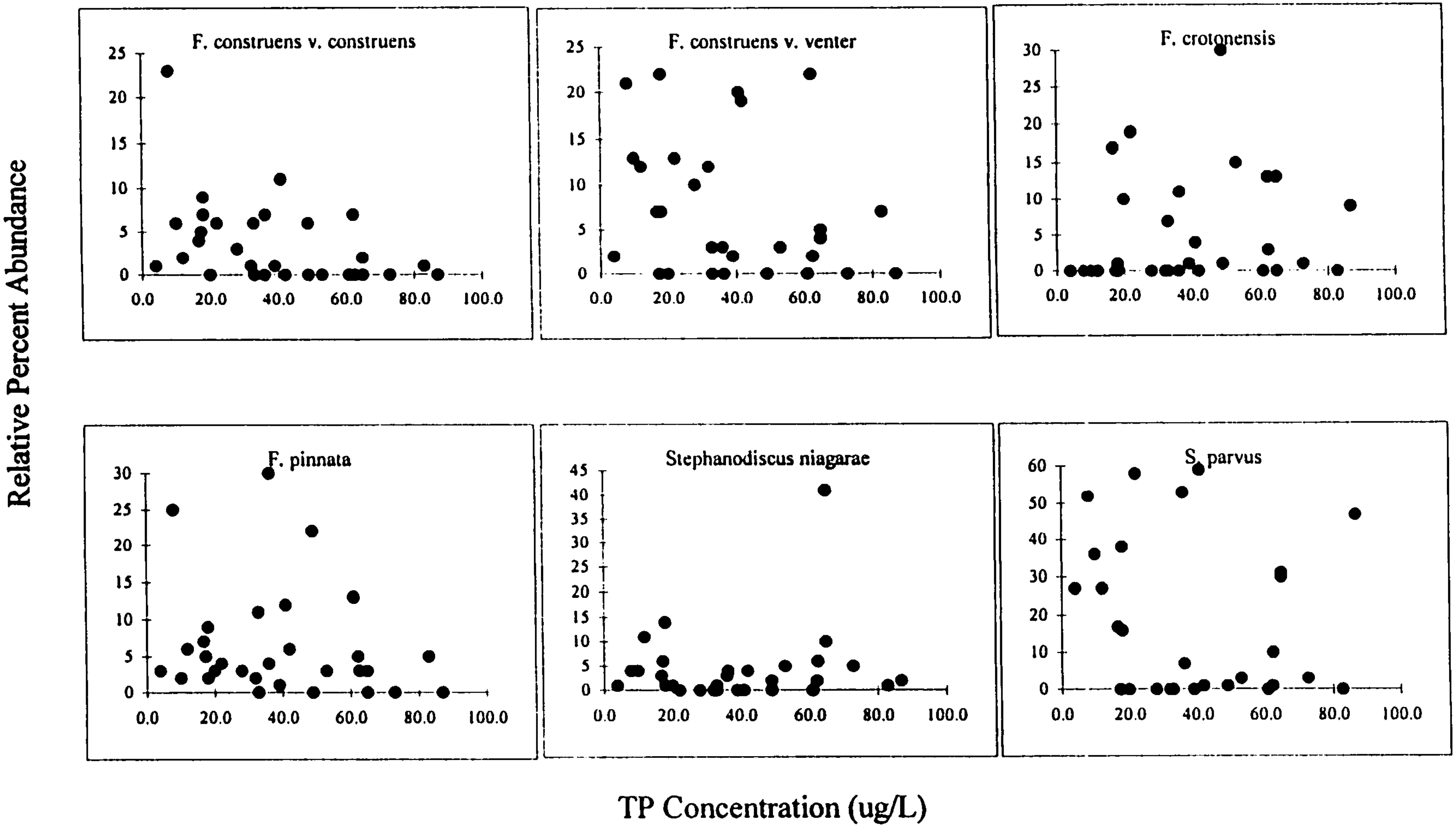


Fig. V-6. continued.

Chapter VI. A model to infer Total Phosphorus Concentrations applied to the sedimentary diatom assemblages from Alberta lakes.

VI.A. Introduction

Palaeolimnology is the study of lake history. Palaeolimnology contributes to the understanding of past climatic changes (Smol *et al.,* 1991). Palaeolimnology is a synthetic science (concerning the historical development of water bodies), but it is also a multidisciplinary science because it makes use of physical, chemical and biological information found in sedimentary profiles (Smol & Glew, 1992).

Characteristics of diatoms such as whole organism preservation, identifications based on cell wall morphology, sensitivity of species to environmental variables, and the tendency to be powerful indicators of past environmental condition, make them a primary component of palaeolimnological studies (Smol, 1988). The use of aquatic organisms in studies provides indirect and direct inferences of lake variables, such as lake water temperature, water depth and salinity (Smol *et al.,* 1995). Lacustrine fossils can potentially provide a more sensitive record of terrestrial palaeoclimates (Smol *et al.,* 1991) because of shorter generation times of aquatic organisms (Smol *et al.,* 1995). Finally, since long-term data are lacking for many ecosystems, lake and pond sediments, and the fossils contained within them, are used to reconstruct past environments (Smol Douglas, 1996).

Traditionally, inferences of lake quality (e.g., nutrient concentration, pH and water level) have been descriptive (e.g., Round, 1957; Haworth, 1969; Hickman, 1979; Hickman & Klarer, 1981; Hickman *et al.*, 1984; Hickman & Schweger, 1993; Hickman & Reasoner, 1994). The known modern ecology of species found in fossil assemblages were summarized and past conditions compared to modern conditions. The fossil species are used as a proxy for environmental conditions. To determine general trends in a lake over a period of time, and to evaluate the influence of human activity on lacustrine environments, this approach remains strong (Anderson, 1994).

The statistical relationship between diatom species and environmental variables has been investigated through many studies (e.g., Hall & Smol, 1992; Christie & Smol, 1993; Reavie *et al.*, 1995a; Korsman & Birks, 1996; Wilson *et al.*, 1996)., Models have been developed that allow rates and magnitudes of change in an environmental variable to be estimated using statistical programs. Thus, inferences in palaeolimnology can now be quantitative (e.g., Birks *et al.*, 1990; Hall & Smol, 1993; Anderson & Rippey, 1994; Dixit *et al.*, 1996). In the last decade, palaeolimnological studies have become quantitative and analytical (Birks, 1998).

To develop quantitative (inference) models, the modern sedimentary diatom assemblages and modern water chemistry measurements from many lakes are analyzed statistically (Dixit *et al.*, 1992). These are known as calibration data sets. An inference model based on species assemblages is developed for the environmental variable that is determined to have the most influence upon species assemblages. Through regression, species optima for the chosen variable are estimated. A formula to estimate the chosen variable, based on the weighted abundance of species is calculated using calibration (Birks *et al.*, 1990). In weighted-averaging regression and calibration, the weights are the relative species abundance in the samples (Cumming *et al.*, 1994). The weighted-averaging approach has been determined to be the best and simplest method to use because it assumes a unimodal response between species abundance along an environmental gradient (ter Braak & van Dam, 1989). In addition, high correlations between observed and inferred environmental values have been produced (e.g., Hall & Smol, 1992; Cumming & Smol, 1993; Wilson *et al.*, 1996).

From the diatom assemblage in a sample, the regression model estimates a site environmental value. This estimate is based on relative species abundance at the site. The regression model can also be used on fossil samples from discreet horizons of a lake sediment core. An underlying assumption is that the assemblage in a single sample (either modern or fossil) is representative of the diatom population in that lake at that time (Dixit *et al.*, 1995). It is also assumed that diatoms from all communities of the lake are randomly mixed and evenly distributed across the lake bottom. Other studies have shown random distribution of species across lake sediments, although shallow water sediments generally have higher abundance of benthic species than deep lakes, and deeper water sediments generally have higher abundance of planktonic species than shallow lakes (Anderson, 1990). An analysis of multiple lake sediment cores from one lake showed the planktonic species assemblage in equivalent horizons to be similar (Blakney, 1998). Abundance of species in the sediment samples did not differ significantly across the lake bottom. Since detailed studies of each lake cannot be done, the results produced from these previous studies form the basis for our assumptions.

A quantitative model to infer lake water total phosphorus (TP) concentration from sedimentary diatom assemblages has been developed (Chapter V). This model can now be applied to infer palaeolimnological TP concentration changes in lakes. Phosphorus is the least abundant nutrient in water (Ruttner, 1974), and often limits biological productivity (Wetzel, 1975) because of a low supply to demand. TP is composed of organic (dissolved and particulate form) and inorganic forms (Ruttner, 1974), but also soluble reactive, soluble unreactive and particulate forms (Gibson *et al.*, 1996. Inorganic phosphorus is the form taken up by plants, yet TP should be the form discussed when interpreting algal productivity (Wetzel, 1975). Dissolved forms of phosphorus (inorganic and organic) and particulate phosphorus circulate through the water column. Inorganic phosphorus is taken up by photosynthetic organisms and eventually excess phosphorus (inorganic and organic) is deposited onto the sediments. TP concentration in the water column will decrease with settlement of particles (Gibson *et al.*, 1996) and by zooplankton and fish consumption (Campbell, 1994). Phosphorus is bound into the sediments and will remain there until the sediments are disturbed and it is re-introduced into the water column. Phosphorus is insoluble in oxygenated sediments (such as in well mixed or oligotrophic lakes), but becomes soluble in anoxic sediments (such as in eutrophic lakes), so it can be continuously re-introduced into the water column of eutrophic lakes (Wetzel, 1975). This of course compounds the problem and allows productive lakes to have continuous algal blooms during the open-water season. The absolute retention of phosphorus by sediments depends on chemical binding capacity (Reynolds, 1996) and by the rate of lake-water hydraulic flushing (Rippey *et al.*, 1997). It has also been observed that in some lakes there is a bimodal seasonal cycle of TP, after ice-out and in late summer, with the latter peak likely related to biological mechanisms such as microbial degradation (Campbell, 1994). It is accepted that the reworking of shallow sediments can release phosphorus into the water column (Gibson *et al.*, 1996; Reynolds, 1996), but as lake levels decrease during dry periods, meso- to eutrophic lakes may be susceptible to accelerated eutrophication (Rippey *et al.*, 1997). This is a factor to consider for some lakes under speculated climatic warming.

Diatoms most often produce blooms in the spring. They are replaced by populations of green algae and then cyanobacteria (Wetzel, 1975). In unproductive (oligotrophic) lakes this is mainly due to silica depletion, but in productive (eutrophic) lakes it is due to higher reproductive rates of these other algae (Wetzel, 1975). Planktonic algae can take up excess phosphorus and store the unused portion (Ruttner, 1974), while benthic algae can utilize the phosphorus stored in sediments (Wetzel, 1983) versus the phosphorus dissolved in the water column. This indicates that there probably is not a simple relationship between algal species and phosphorus concentrations in the water. Other factors such as conductivity may influence diatom species and the relationship to TP concentration (Reavie *et al.*, 1995b). These underlying factors must be considered when using a mathematical model based on species assemblages to infer epilimnetic TP concentration in a lake.

There were four objectives of this study. First, a previously developed model for inferring total phosphorus concentration (Chapter V) was applied to the palaeolimnological record of seven Alberta lakes to assess its usefulness. This has never been attempted before on diatom sedimentary records from lakes in Alberta. The model was developed from a set of Alberta lakes, and it was thought that by using lakes from the same area that a possible control for underlying factors such as geology, catchment vegetation, and dominant climate patterns would be made. Second, since the palaeolimnological record of these lakes has been previously described by qualitative methods, a comparison between qualitative and quantitative approaches could be made. Rates and magnitudes of changes in TP concentration can be estimated by quantitative method, and it will be determined if more information is provided by this method than by qualitative methods. Third, by using the records from seven Alberta lakes (eight long sediment cores in total) any limitations of quantitative methods could be discovered and discussed. There must be some records, or parts of some records, which cannot be used to infer TP concentration, due to the absence of species from modern samples, and the lack of estimated TP optima concentration for those species. Finally, I wanted to evaluate the possibility that some lake records are better suited for quantitative palaeolimnological methods than are other records. Should some lakes be disqualified from palaeolimnological studies because they do not meet *a priori* requirements?

VI. B. Study Area

The province of Alberta is divided into several ecoregions. These are defined primarily by geographic and climatic features (Crosby, 1990), because these influence the vegetation and soils, that develop in an area. The ecoregions of Alberta have been mapped and described by Strong and Leggat (1981). The ecoregions, the coring location for the eight long lake sediment records (from 7 lakes) (A – H) and the 30 lakes used to derive the TP calibration model are indicated on a summarized map of Alberta (Fig. VI-1). The geographic location of the lake cores and general information is given in Table VI-1, while the location of the 30 calibration lakes and summarized lake data is given in Table VI-2. The location of six climate stations (I – N) and detailed information are also given (Fig. IV-1; Table VI-3). These values are based on 30-year climate normals (Atmospheric Environment Service, 1993). Annual total precipitation (mm) (Fig. VI-2a) and mean July temperature (°C) (Fig. VI-2b) (Atlas of Alberta, 1984) for the province are summarized. The annual total precipitation in the northern to central regions is generally higher than in the southern regions. Northern Alberta, along with mountain and foothills regions, experience cooler summer temperatures than the southern portion of the province. As a result dense forest tends to develop in the northern, mountain and foothills regions, open parkland to grasslands tend to develop in the central region, and dry grassland tends to develop in the southern region (Fig. VI-1).

Much of the vegetation of the Boreal Forest consists of trees including *Betula balsamifera, Populus tremuloides, Pinus banksiana, Picea glauca,* and *P. mariana.* The importance of each tree species in the catchment of a lake is influenced in general by precipitation, evaporation and soil type. Wetlands and peatlands also occur in the Boreal Forest region, and in some areas, open peatlands, instead of dense forests, occur over large areas (Halsey *et al.*, 1997). The Montane Boreal Forest typically has *Pinus banksiana, Picea glauca*, and *P. mariana* as the dominant tree species. Finally, the Aspen Parkland typically has *Populus tremuloides* as the only tree species, combined with a large variety of grass species. This area is typically drier due to more evaporation than the more northerly Boreal Forest. In addition, decomposition rates are generally higher, thus limiting moss accumulation (Zoltai & Vitt, 1990). Stands of trees in the

Aspen Parkland can vary from dense forests in the northern and western regions, to open groveland in the southern and eastern portions of this ecoregion. This ecoregion is variable in runoff, and as a result lake levels can vary from year to year (Crosby, 1990).

The Boreal Forest region of Canada (Rowe, 1972) occupies approximately the northern two thirds of the province, and has been divided into five ecoregions by Strong and Leggat (1981). Long sediment cores were taken from seven lakes that are located in three of these ecoregions (Boreal Forest, Montane Boreal Forest and Aspen Parkland). Lakes that were included in the calibration model were located in the same ecoregions,. Most of the calibration lakes (n=14) were located in central Alberta, around the Boreal Forest – Aspen Parkland transition region (Fig. VI-1), but some lakes from the extreme north (n=3), northeast (n=9), west (n=2), and central Alberta (n=2) were also included.

VI.C. Methods

VI.C.1. Sampling

Details on core location, core extraction methods, sampling frequency for diatom analysis, sample volume for diatom analysis, and radiocarbon dates can be found in the appropriate reference (Table VI-1).

Modern lake samples used in the inference model were sampled by personnel at Alberta Environment (n=28) and the Limnology Lab, University of Alberta (n=2). Samples for surficial sediments and water chemistry were taken from the deepest part of each lake. Details on sediment and water chemistry sampling, storage and analysis are provided in Chapter V.

VI.C.2. Laboratory Analysis

Samples for diatom analysis from the lake sediment cores ranged in size from 0.5 to 1.0 cm^3. Sampling frequency varied with the core depending on presence or absence of a tephra layer or absence of segments in a core. From the modern lake sediment samples, 1.0 cm^3 of sediment was removed for diatom analysis. These samples were treated with $K_2Cr_2O_7$ and H_2SO_4 to remove all organic matter (Hickman *et al.*, 1984). The diatom slurry was then washed with deionized water until there were no traces of acid. Aliquots of 0.02 - 0.35 mL were pipetted onto coverglasses, air dried slowly to ensure even distribution of valves across the coverglass, and then fixed permanently in Hyrax.

A minimum of 500 diatom valves was counted on each slide at 1000x using oil immersion. Identifications were made using Germain (1981), Hustedt (1930), Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), and Patrick and Reimer (1966, 1975).

VI.C.3. Inference Model

An inference model for estimating epilimnetic total phosphorus (TP) concentration from the diatom assemblage in a sediment sample was derived by Weighted Averaging (WA) regression and calibration. In WA regression, optimal TP concentrations are estimated for each species. This is calculated from the occurrence of the species in many samples and the concentration of TP in each sample (epilimnetic measurement) of the calibration data set. WA calibration performs the opposite procedure. TP concentration for a sample is estimated from the species composition in the sample and the estimated TP concentration optimum for each species. The "weight" in WA refers to the relative abundance of a species in a sample (Cumming and Smol, 1993). The computer program WACALIB version 3.3 (Line *et al.*, 1994) was used to perform the regressions and calibrations. Details of steps followed to develop the inference model can be found in Chapter V. This formula was applied to the fossil diatom assemblages found in eight lake cores. These were the same cores used for qualitative palaeolimnological analysis.

VI.C.4. Analogue Matching

The reliability of fossil TP concentration estimates is related to the similarity of fossil assemblages to modern calibration assemblages. Estimates of TP concentration should be more accurate for fossil samples with modern analogues than for fossil samples without modern analogues (Birks *et al.*, 1990). The program ANALOG 1.6 (J.M. Line and H.J.B. Birks, unpublished program) was used to determine the similarity of the fossil samples to the modern calibration samples. Various dissimilarity coefficients can be used to determine if fossil samples have a close modern analogue. Samples without close modern analogues have unusual species assemblages, or they have a species with abundance outside of the range recorded in the modern samples. A squared χ^2 dissimilarity coefficient was used by Hall & Smol (1993), Reavie *et al.* (1995a) and Hall *et al.* (1997) to determine which samples lacked good modern analogues. This method compares the presence and absence of species in sample units, and tests to determine if the occurrence of two species are independent (Ludwig & Reynolds, 1988).

VI. D. Results and Discussion

The Holocene diatom palaeolimnological record for each of these lakes has been described previously (see Table VI-1 for references). A model to infer total phosphorus (TP) has been developed from modern lake sedimentary diatom assemblages and epilimnetic TP concentrations (Chapter V). This model has been applied to the fossil diatom species data from these same eight long lake sediment cores from seven lakes. Summarized diatom stratigraphies, inferred TP concentrations, number of species used and percentage of the diatom assemblage used to infer TP concentration for samples in the lake cores are given (Fig. VI-3 to VI-10).

Optimal estimates for each diatom species can only be determined if the species occurs in the modern calibration data set. Therefore, only fossil species also found in the calibration set will have estimates of optimum TP concentration. If a species is unique to fossil samples it cannot be used to estimate TP concentration for the sample. For each fossil sample the percentage of the diatom assemblage used to estimate fossil TP was determined. This indicated the similarity of the fossil assemblage to the calibration assemblage. Fossil samples were also compared to modern samples by squared χ^2 analogue matching. Fossil samples without good modern analogues (significantly different assemblages) were determined. Estimates of TP concentration for these samples were considered unreasonable due to the dissimilarity of the fossil species assemblage to modern species assemblages. For each lake core, qualitative and quantitative palaeolimnological methods were compared.

VI. D. 1. Otasan Lake

Inferred concentrations of TP were fairly constant (approximately 20 μg TP/l) for most of this record (Fig. VI-3). The number of species used to infer TP concentration over this record was similar in all samples. Benthic species dominated between 320 to 240 cm and 145 to 0 cm, while planktonic species dominated between 235 to 145cm. Between 235 to 195 cm (*ca.* 6100 to *ca.* 5000 years BP) the highest concentrations of TP (27.4 to 34.0 μg/l) were calculated. Qualitative interpretations (based solely on the dominant species in the assemblage) also inferred higher lake nutrients during this time (Chapter II). The most abundant diatom species at that time were *Stephanodiscus niagarae, Aulacoseira ambigua* and *A. italica*. Estimated optimum TP concentrations were higher for the first two species (47.86 & 43.39 μg/l) than for the latter species (33.99 μg/l) (Table VI-4). These are mesotrophic to eutrophic indicator species based upon estimated TP concentration optima (Hall & Smol, 1992; Fritz *et al.*, 1993; Bennion, 1994; Reavie *et al.*, 1995a). Before and after this zone both inferred nutrient level and inferred TP concentrations were lower. Both qualitative and quantitative inference methods were very similar for this lake record.

In most samples at least 80 % of the diatom population was used to estimate TP concentration. In the lower-most samples (320 – 280 cm), unusual species assemblages were encountered. *Ellerbeckia arenaria* (an important species of these assemblages) was not found in the modern calibration samples, and therefore estimates of optimum TP concentration for this species were not determined. Interpretations of TP concentration for these lower-most samples were based on a smaller portion of the assemblage than in other samples from the core. Samples 300 cm and 310 cm had high but not significant squared χ^2 dissimilarity coefficient values. Samples 310 and 320 cm were unusual, but not extremely unusual. Most of the other species found in the samples were similar to species combinations found in the modern calibration lake samples, and the independence of species was rejected, and so it was determined that all samples had modern analogues.

VI. D. 2. Mariana Lake

Planktonic and benthic algal assemblages fluctuated in importance over this record. Planktonic species dominated between 600 to 535 cm and 417 to 205 cm, while benthic species dominated between 535 to 417 cm and 200 to 0 cm. An unusual mix of benthic and planktonic species occurred between 673 to 600 cm. Inferred TP concentrations remained fairly constant and low over the whole record (3.85 to 29.08

μg/l) except for one zone (23.61 to 39.77 μg/l) from 420 to 205cm (*ca.* 4300 to *ca.* 2700 years BP) (Fig. VI-4). Based on the species assemblage alone, lake nutrient status was inferred to have been highest at that time (Chapter III).

Most of the species found in the fossil samples were also present in the calibration lakes. Thus, inferred TP concentration for most samples was based on more than 85 % of the total diatom assemblage, even though the total number of species used to infer TP concentration did fluctuate over this record. There were some samples with fewer species in common with the modern samples. For example, at 540 cm only 43 % of the assemblage was used to infer a TP concentration of 9.58 μg/l. At 530 cm, 87 % of the assemblage was used to infer a TP concentration of 8.17 μg/l. These estimates varied little even though percent of the assemblage used to calculate TP concentration for the sample varied greatly.

Quantitatively inferred TP concentration and qualitatively inferred nutrient levels agreed for this lake record. This lake has always had low phosphorus values except for the period between 420 to 205 cm. During this peak of TP concentration, the number of diatom species used in the model was low, even though in most of the samples these species represented 80 to 100 % of the total assemblage. *Aulacoseira ambigua* dominated the species record between 420 to 205 cm, and thus inferred TP concentration was based heavily upon the abundance of this planktonic species. As discussed above this species had a high value for optimum TP concentration (Table VI-4), and it is an indicator of mesotrophic to eutrophic status.

Species diversity was not particularly high for most samples of the core, but especially during the zone of highest inferred TP concentration. Low species diversity has also been recorded for other eutrophic lakes (Bradbury & Waddington, 1973; Blakney, 1998). Eutrophication has been inferred for other lake records when *A. ambigua* dominated the diatom assemblages (Hall & Smol, 1993). A decrease in TP concentration, and a change to oligotrophic to mesotrophic status was inferred after 205 cm (*ca.* 2700 years BP) until the present, when *A. ambigua* decreased in importance and was replaced by benthic *Fragilaria* species. High squared χ^2 values were computed for samples 540, 545 and 552.5 cm, but they were not significant. These assemblages were slightly different, but species occurrences were not independent. All samples from this core were analogous to the modern calibration samples.

VI.D.3. Spring Lake

Estimated concentrations of TP were low and varied little over the whole record from this lake (Fig. VI-5). In most samples from Spring Lake more than 85 % of the assemblage was used to estimate TP concentration, but the number of species comprising those assemblages fluctuated over the core. Through qualitative interpretations, eutrophic status was inferred between 260 to 210 cm, with general increasing productivity after *ca.* 10,000 years BP (390 cm) (Hickman & White, 1989). Benthic species dominated the diatom assemblages except in a few samples between 260 to 210 cm when planktonic species, mainly *Stephanodiscus hantzschii*, dominated. This is a eutrophic indicator species (Hustedt, 1949; Bradbury, 1975; Hickman, 1979; Hickman & White, 1989; Hall & Smol, 1992; Fritz *et al.*, 1993; Bennion, 1994; Reavie *et al.*, 1995b), yet high concentrations of TP were not calculated for these samples when it was the dominant species. This is possibly due to the rarity, and low occurrence of this species in the calibration lakes (Table VI-4). This species only occurred in 2 of the 30 calibration lakes, and at no more than 4 % relative abundance in either of those lakes.

For this lake record quantitative estimates of TP concentration completely disagreed with qualitative interpretations of trophic status. This was possibly due to the rarity of *Stephanodiscus hantzschii* in the data set, the subsequently poor estimates of TP concentration in samples where this species dominated, and the reliance upon one species in descriptive interpretations. Analogue matching (squared χ^2) identified sample 260 cm as significantly different from modern samples. This sample was overwhelmingly dominated by *S. hantzschii* (86.9 %). *S. hantzschii* has a poor relationship to TP concentration in this data set and cannot be used reliably in estimates of TP concentration. All other samples were similar to modern calibration samples.

For the remaining samples of the core, 430 to 270 cm, and 200 to 5 cm, benthic species dominated the assemblages. These were predominantly small epipelic *Fragilaria* species. Inferred TP concentrations for these samples were low, while pigment data from these sediments suggested gradually increasing nutrient status (Hickman & White, 1989).

This suggests that these cosmopolitan epipelic species were poorly correlated to water chemistry. These data suggest that inferences of epilimnetic water are inaccurate when based predominantly on epipelic algal species. Anderson *et al.* (1993) also noted poor associations between some benthic diatom species and TP concentration in epilimnetic water.

VI.D.4. Lake Wabamun – Moonlight Bay

This core was taken from a shallow region (2.0 m) of Lake Wabamun (Hickman *et al.*, 1984). This was an interesting record due to the absence of diatoms in some sections (910 – 875 cm; 865 – 795 cm; 725 – 595 cm; 570 – 530 cm), the very low diatom species diversity in some samples (990 cm; 975 cm; 790 cm; 750 cm; 740 cm; 730 cm; 590 cm; 575 cm), and the overwhelming dominance by benthic species over most of the core (550 – 0 cm). These benthic assemblages were dominantly epipelic (70 – 80 %; 550 - 60 cm) and then dominantly epiphytic (70 - 80%; 50 - 0 cm). Planktonic species dominated between 1050 to 915 cm as *Stephanodiscus* species and as *Cyclotella* species between 945 to 915cm.

The number of species from the fossil samples used to infer TP concentration was very low (less than 10 in many samples) even though they represented more than 80 % of the diatom assemblage (Fig. VI-6). There were some samples (870 – 575 cm) that had very few species (5 or less) in the assemblage. These few species still represented more than 80 % of the diatom assemblage. Estimates of TP concentration for these samples were based on the estimated optima of very few diatom species and were circumspect.

High concentrations of dissolved TP were estimated when planktonic species dominated the assemblages, primarily *Stephanodiscus niagarae* and *S. hantzschii*, (1050 – 940 cm). When low concentrations of TP were estimated (935 – 75 cm), initially *Cyclotella* species and then benthic species (primarily *Fragilaria construens*, *F. construens* var. *venter*, and *F. brevistriata*) dominated the assemblages. Traditionally, these species have been described as eutrophic and oligotrophic indicators, respectively (Anderson *et al.*, 1993). Based upon fossil diatom species and pigment data, the lake was interpreted as mesotrophic (1067 – 800 cm), then oligotrophic (750 – 450 cm) and then gradually eutrophic (450 – 0 cm) (Hickman *et al.*, 1984; Hickman & Schweger, 1991b).

High TP concentrations were estimated for the first portion of the core (1050 to 945cm), while low TP concentrations were estimated for the remainder of the core (945 to 0cm). Model interpretations agreed with subjective interpretations for the portions of the core when planktonic species dominated.

There were peaks of planktonic species (mainly *S. hantzschii*) between 870 to 730 cm. Total diatom numbers (Hickman *et al.*, 1984) and number of species were very low, while pigments of cyanobacteria were high (Hickman & Schweger, 1991b) for this zone. This indicates high lake productivity and most likely high phosphorus at this time. Diatom-inferred TP concentrations during this zone were average in comparison to estimates for the whole core. Two samples between 870 to 730 cm had poor modern analogues (as determined by using squared χ^2 index) and thus estimates of TP concentration were not considered to be accurate. Diatom assemblages are commonly consistent above 300 μg TP/l due to few species surviving under high TP and low silica conditions (Anderson *et al.*, 1993).

Based on species data and fossil pigments, eutrophic status was inferred for the latter portion of the core (450 to 0cm) (Hickman *et al.*, 1984; Hickman & Schweger, 1991b), while the model estimated low TP concentrations for this portion of the core. Diatom species diversity and diatom numbers were high (in comparison to other samples in the core). The assemblage was dominated by epipelic species (550 – 50 cm) and then by epiphytic species (50 – 0 cm). For these zones, 75 to 100 % and 55 to 75 %, respectively, of the total assemblages were used to infer TP concentration. Thus, most of the species in the assemblage were used in the model, and only a few of these samples had no modern analogues. Low diatom-inferred TP concentrations, based on the benthic species in these samples, is a contrast to interpretations of eutrophic status, based on diatom assemblages and fossil pigments. As observed for Spring Lake, the relationship between benthic species and water chemistry is poor, thus making inferences about nutrient status of the lake water inaccurate.

VI.D. 5. Lake Wabamun – Seba

This core contrasts with the core from Moonlight Bay in that it was taken from deeper water (10.0 m), and the record was dominated by planktonic species (Hickman *et* *al.*, 1984). Some sections of this core were not retrieved (793 – 693 cm; 497 – 397 cm). Total diatom numbers were moderate (1420 – 1245 cm), to very low (1245 – 390 cm) to high (390 – 0 cm). Species diversity (although higher than in the Moonlight Bay core) was low in some sections of this core (1350 – 1150 cm; 1125 – 610 cm) (Fig VI-7). Planktonic species dominated (50 to 80 %) over most of this record, although there were fluctuations between benthic and planktonic dominance between 1220 to 1130 cm, 1020 to 810 cm, and 690 to 600 cm. In the lower portion of the core (1420 – 1220 cm) fewer species (5 – 10) were used to infer TP concentration, while in the upper portion of the core (390 – 40 cm) more species (10 – 20) were used to infer TP concentration. This variation in number of species still represented an average of 90 % of the diatom population in most samples. Highest TP concentrations were inferred in the lower portion of the core (1420 – 1220 cm), while moderate TP concentrations were inferred in the upper portion of the core (390 – 40 cm). Inferred TP concentrations were higher for the Seba record than for the Moonlight Bay record, but estimates of TP concentration in the former were based mainly on planktonic species.

Qualitative interpretations (based on total chlorophyll *a* pigments and diatom numbers, and species assemblage) suggested eutrophic status in the first stages of the lake (until 1200 cm) (Hickman *et al.*, 1984; Hickman & Schweger, 1991b). This was followed by oligotrophic status in the middle of the core (until 500 cm), and finally mesotrophic status from 500 cm to the top of the core. Interpretations from the calibration model also inferred these conditions. High TP concentrations were inferred (47.57 – 136.41 µg/l) when *Stephanodiscus niagarae* was the dominant species (1404 – 1245 cm). As it decreased in importance and was replaced by *S. hantzschii* inferred TP concentration also decreased (1175 – 670 cm). Estimates of optimum TP concentration were higher for *S. hantzschii* than for *S. niagarae* (Table VI-4). The latter species occurred widely in the data set, and had higher relative abundance in samples than the former species. It was inferred that *S. niagarae* had a better correlation to TP concentration in this data set than *S. hantzschii*. Diatom-inferred TP concentrations for the samples with higher populations of *S. niagarae* should be more accurate than samples with higher populations of *S. hantzschii*.

Higher concentrations of TP were estimated between 800 to 500 cm from the inference model. Estimates of TP concentration between 1090 to 390 cm were circumspect due to poor diatom preservation (very low valve numbers and species diversity). Also many of the samples in this zone had extremely different assemblages (significant squared χ^2 values). In addition large populations of cyanobacteria were present in the lake at this time (Hickman & Schweger, 1991b). Since cyanobacteria often dominate in high phosphorus lakes, eutrophic to hyper-eutrophic status was suggested between 700 to 550 cm. High diatom populations would not be expected under these conditions (except possibly in early spring assemblages). The very low total number of diatom valves but high abundance of eutrophic indicator diatom species (*Stephanodiscus niagarae*, *S. hantzschii*, *Aulacoseira ambigua*, and *A. granulata*) may be a reflection of high phosphorus levels at this time. Also *S. hantzschii* is a common species in eutrophic lakes and occurs in some culturally eutrophied British Columbia lakes (Reavie *et al.*, 1995b). The dominance of this species in samples with very low diatom and species numbers, and very high concentrations of cyanobacteria pigments, all suggest that the lake had very high concentrations of nutrients at this time. When cyanobacteria dominate an algal assemblage, a diatom based TP concentration inference model can not accurately estimate phosphorus concentrations, although actual phosphorus levels would have likely been very high and outside of the range of the model.

After 390 cm, total diatom numbers increased, along with the number of species used to infer TP concentration. In the samples towards the top of the core (after 200 cm), there was a trend of gradually decreasing TP concentration. Initially *S. niagarae* dominated, but then *Aulacoseira ambigua* dominated after about 390 cm. *A. ambigua* had a lower estimated optimum TP concentration than *S. niagarae* (Table VI-6). Moderate TP concentrations were inferred for this latter zone when *A. ambigua* dominated.

Evidence from the diatom record, diatom to stomatocyst ratio, and pigments of cyanobacteria (Hickman & Schweger, 1991b) and now this TP concentration model suggest that the lake has been less productive over the last 2500 years as compared to earlier times in the lake history.

There was better agreement between qualitative and quantitative inferences for the Seba core than for the Moonlight Bay core. This was probably due to the higher abundance of planktonic species in Seba core. Interpretations based on planktonic species seem to be consistent between inference methods (qualitative versus quantitative), probably due to the consistency of ecological information about these species, and their direct association with the water column (and all dissolved components).

VI.D.6. Fairfax Lake

Both benthic and planktonic species were present in this lake but the relative proportions of the communities changed over the length of the core (Hickman & Schweger, 1991a). Based on fossil pigments and diatom species assemblages, the lake was described as eutrophic prior to 500 cm (*ca.* 7000 years BP), and oligotrophic to mesotrophic from then until the present (Hickman & Schweger, 1991a). The epipelic community (small *Fragilaria* species) was dominant throughout, except between 460 to 210 cm, when planktonic species dominated the assemblages (Fig. VI-8). The species in this zone, present in varying amounts, are oligotrophic indicators (*Cyclotella radiosa, Tabellaria fenestrata* and *Fragilaria crotonensis*) and eutrophic indicators (*Aualcoseira ambigua* and *Stephanodiscus niagarae*) (Anderson *et al.*, 1993; Agbeti & Dickman, 1989; Hall & Smol, 1992; Fritz *et al.*, 1993; Reavie *et al.*, 1995a), but the oligotrophic species were more abundant. Inferred TP concentrations (based on estimated TP concentration optima and relative abundance of these species in the samples) was moderate during this zone (as compared with all concentration estimates over the core) (Fig. VI-8). After 205 cm, the assemblages were composed predominantly of benthic species, and diatom-inferred TP concentrations were low.

Highest diatom-inferred TP concentrations were between 700 to 605 cm (*ca.* 11,100 to ca. 9100 years BP). Prior to and after these levels, moderate concentrations of TP were calculated, while after *ca.* 160 cm (*ca.* 2000 years BP) slightly lower TP concentrations were calculated. Eutrophic status was qualitatively inferred for the whole zone from 700 to 500 cm, but diatom inferred TP concentrations decreased to moderate to low values after 605 cm. TP concentration estimates after 605 cm were based on a dominant benthic community. The contrast in qualitative versus quantitative interpretations may again reflect the poor correlation between benthic species and water chemistry. From these lines of evidence (pigments contrasted with diatom-inferred TP concentration) it is suggested that the large presence of benthic species did cause an underestimation of inferred TP concentration here, as they may have done in Spring Lake and Lake Wabamun (Moonlight Bay).

Lowest inferred TP concentrations, and oligotrophic status (Hickman & Schweger, 1991a), occurred in the uppermost portion of the core (185 – 0 cm). This is when the epipelic community dominated and planktonic species represented only 20 to 30 % of the assemblages. Both quantitative and qualitative interpretations suggested that lake nutrient levels were low for the upper 185 cm of the core (the last *ca.* 2500 years). When diatom-inferred TP concentrations are based predominantly on benthic species, and estimate values are low, inaccurate inferences may be suspected. In some cases these inferences are accepted because other lines of evidence (e.g., sedimentary pigments) also suggest the same conditions. Overall for this lake record both quantitative and qualitative interpretations were similar.

VI.D.7. Goldeye Lake

This core was taken from a water depth of 14.0 m. It was over 4.0 m in length, and it represented more than an estimated 15,000 years of lake history (Hickman & Schweger, 1993). The first 1.0 m of the core had saline diatom assemblages. Saline lakes and species were not a part of the calibration set, and thus this portion of the core was omitted because there were very few species in common between the core and the calibration set. Freshwater fossil species from this portion of the core represented very low percentages of the total fossil assemblages, and thus TP concentration estimates would have been extremely inaccurate.

Since 10,400 years BP (350 – 0 cm) only freshwater diatom species have occurred in this lake (Hickman & Schweger, 1993). Interpretations for TP concentration are based only on the fresh water diatom species from 250 to 0 cm because of only freshwater diatom species present in the calibration model. Estimated concentrations of TP over this record showed some fluctuations, but no overall trend (Fig. VI-9). This suggests that phosphorus levels have not changed very much, and that this lake has been oligotrophic for at least 5000 years. Hickman and Schweger (1993) concluded that the palaeolimnological record has been stable since *ca.* 10,400 years BP.

The number of species used to infer TP concentration in each sample was generally high, with little deviation in number over the whole core. The species used to infer TP concentration represented 55 to 87 % of the total assemblage. The percent of the assemblage used to estimate TP concentration in these samples was generally lower than the percent of the assemblage used in samples from other lake cores. On average, 70 % of the assemblage was used to estimate TP concentration. Clearly some of the fossil species in these samples were not a part of the calibration set.

This lake presently has a large flat bottom (at an average depth of 9.0 m), and a margin with abundant macrophytes. The phytoplankton is the dominant assemblage, but the lake also has well-developed epipelic and epiphytic algal communities (Hickman, unpublished data). There is thus an unusual mix of communities in this lake, and in the fossil sediments. Qualitative and quantitative interpretations are similar for this record, but inferred TP concentration was unremarkable compared to records from other lakes.

VI.D.8. Cooking Lake

The core from this lake was 380 cm long, represented *ca.* 5200 years, but diatom valves were not encountered until 175 cm (Hickman, 1987). Estimated TP concentrations fluctuated, but were high between 175 to 20 cm (but with some fluctuations) and low in the upper two samples (Fig. VI-10). The number of species used to estimate TP concentration in each fossil sample was fairly low (between 7 and 17). Species diversity was low, as it is in other eutrophic lakes (e.g., Bradbury & Waddington, 1973). In all but 4 samples, at least 90 % of the total diatom assemblage was used to estimate fossil TP concentrations. The high correlation between species of the fossil samples and calibration samples (observed visually and determined statistically through analogue matching) indicated that estimates of TP concentration were reasonable. It was determined through squared χ^2 analysis that all samples had good modern analogues. This record was dominated by planktonic species, mainly *Stephanodiscus niagarae* (up to 80 % in some samples). The estimated TP concentration curve largely followed the relative abundance of *S. niagarae* in this core. This species had the fourth highest inferred optimum TP concentration (47.86 µg/l) of all species in the inference model (Table VI-4). This explains why inferred TP concentrations were high for most of this record. A decrease in diatom-inferred TP concentrations occurred as the planktonic community decreased to 20% abundance, and the benthic community (epipelic and attached) increased to 80% abundance.

Based on diatom-inferred TP concentrations, phosphorus was very abundant since *ca.* 2900 years BP until the last few hundred years when it became moderately abundant. Catchment vegetation around this lake has remained stable since *ca.* 2900 years BP, and preserved fossil pigments and diatom assemblages indicated high lake productivity over this whole record (Hickman, 1987). Presently this lake is eutrophic (Hickman, 1987), and the planktonic community is more important than the epipelic (benthic) community (Hickman, 1978). The diatom species from the top of this sediment core were predominantly benthic. Thus, the dominant algal community (which is planktonic and composed of species of Chlorococcales, cyanobacteria and diatoms) is not represented by these upper core samples. The decrease in inferred TP concentration at the top of the core is probably not accurate. Species of Chlorococcales and cyanobacteria typically occur under high phosphorus levels, and can out-compete diatom species. Only diatom species were used to infer TP concentration. The other algal species, which make up a larger portion of the total algal assemblage (Hickman, 1987) were not included in the model. Thus, a very small percentage of the total algal population from Cooking Lake was used to infer TP concentrations. This may explain the discrepancy between modern eutrophic conditions (based on the high population of green algae and cyanobacteria) currently in this lake, and model estimations of lower TP concentration. Alternatively, TP concentration may have increased significantly very recently.

Quantitative (inferred TP concentration) and qualitative (diatom species assemblage and fossil pigments) approaches generally agreed for this lake except at the top of the core when a benthic community dominated the assemblage. The assemblages in these upper samples were not significantly different from the assemblages in the calibration samples. All diatom based inference models are limited when diatom species represent a very small component of the entire algal assemblage in a lake.

VI.E. General Discussion and Synthesis

Inference models are applied to the sedimentary fossil assemblages in a lake core to estimate change over the history of the lake (Anderson *et al.*, 1993). The quantitative relationship between diatom species and water chemistry variables such as pH (e.g., Birks *et al.*, 1990), salinity (e.g., Fritz *et al.*, 1991; Cumming & Smol, 1993; Wilson *et al.*, 1996), phosphorus (e.g., Hall & Smol, 1992; Fritz *et al.*, 1993; Anderson *et al.*, 1993), and dissolved organic carbon (Pienitz & Smol, 1993) have been investigated and proven to be statistically significant. The models derived from these various studies have been applied to sedimentary diatom assemblages from lake cores and used to infer down core changes in the variable. These models are used on both short and long term sedimentary records. Diatom assemblages, and palaeolimnological inferences derived from them, are a proxy for environmental condition.

Palaeolimnological methods (either qualitative or quantitative) are often the only way to make inferences about (pre-disturbance or pre-historical) lake development. Inference models are effective because changes can be quantified however there are limitations. Inference models are derived from a set of lakes within one area. Typically sites of palaeolimnological study are also located within this area to eliminate underlying influences such as bedrock type and predominant climate patterns. Inference models are only applicable for a certain range of the variable. This is based on the range in the calibration data set. Even if the modern measured value of the lake variable is within the range of the data set, it is quite likely that at some time in the past actual values were outside of this range. Estimates of the variable for such samples would be inaccurate.

Calibration data sets and inference models are based on relative abundance of species in the lakes. The distribution and abundance of species in a calibration data set is variable. Some species are widely distributed and abundant in many lakes, while some species are common in the data set but are rare in most lakes. Some species found at higher abundance in some of the fossil samples than in all of the calibration samples include *Cocconeis placentula, Fragilaria construens* var. *construens, F. construens* var. *venter, Stauroneis anceps, Stephanodiscus hantzschii* and *S. niagarae*. Other species may be rare in the data set but very common in one or two lakes, and finally some species are both rare in the data set and rare in the few lakes in which they occur. These rare species are often very sensitive to environmental parameters and may provide useful information (Birks, 1998). These variations in species relative abundance across the lakes in the calibration set affect the usefulness of the species in the model. For example, *Stephanodiscus hantzschii* was rare in the data set (it occurred in two lakes) and occurred at low relative abundance (maximum = 4 % in those lakes), but in many fossil samples it occurred as a dominant or sub-dominant species. Estimates of TP concentration for samples in which this species was very abundant were typically considered unreliable. By using analogue matching, these kinds of samples are identified. The samples have no analogue in the modern calibration set, and thus adequate interpretations are unlikely. In contrast, *S. niagarae* was more common in the data set (in 22 lakes) and occurred up to 41 % relative abundance in some samples. This species was also common in many fossil samples, and because of its common occurrence in the modern samples estimates of TP concentration for those sorts of samples were considered more reliable.

A consideration to be made is if estimates of TP concentration for fossil samples based on rare to moderately abundant calibration species are as accurate as estimates based on abundant calibration species. The accuracy of estimates of TP concentration optima for species is a function of species distribution across many lakes, relative abundance of the species in those lakes, and similar relative abundance of the species between lakes. Estimates of TP optima concentration and estimates of tolerance are more accurate and narrower, respectively, if the species occurred with equal abundance in lakes with similar chemistry (ter Braak & van Dam, 1989).

Poor estimates of an environmental variable (e.g., TP concentration) for one or many samples from a lake core occur when non-analogue fossil assemblages are found. If an important fossil species is not present in the calibration lakes, then an estimate of optimum TP concentration is not possible. Estimates of fossil TP concentration will not include that particular species. This occurred in Otasan Lake. *Ellerbeckia arenaria*, an important species in the lower most samples (320 – 285 cm) was not found in any of the observed modern samples (Chapter II, Chapter IV). This species was an important component of an unusual assemblage. Likewise, the lower portion of the core from Goldeye Lake was dominated by saline species. Saline lakes were not a part of the calibration set, and so these lower-most samples were non-analogous to the calibration lakes. If saline lakes had been examined it is likely that many of the fossil species would have also been found in the modern samples. The upper samples from Goldeye Lake represented an unusual mix of benthic and planktonic species, but this was due to the morphometry of the lake basin and not necessarily to the chemistry of the water. This combination may be unusual, but may occur in other lakes. It is likely that the flora is analogous to other modern assemblages, although not to the assemblages in these calibration lakes.

For all of these records the number of species used to infer fossil TP concentration was given. This represents the number of species in common between the fossil and modern samples, and it varied within and between the cores from the seven lakes. In some of the samples inferred TP concentration was based on only a few species, and in these samples the low number of species represented between 40 to 100 % of the total diatom assemblage. In some samples from Lake Wabamun (both cores) the few species found represented 60 to 90 % of the assemblage. Estimates of TP concentration for these samples were questionable because they were dependent upon the abundance of three to five species. In samples with low to moderate species diversity (less than 10 species), one species quite likely overwhelmingly dominates the assemblage. Inferred TP concentrations were calculated from the weighted-abundance of species in a sample. Inferred TP concentration will be highly influenced by a dominant species, and thus estimates of TP concentration for the sample will be close to the estimated TP concentration optimum for that species. According to the theory behind weighted-averaging methods, a species will be most abundant when environmental conditions are close to optimum for that species (ter Braak & van Dam, 1989). In the samples dominated by one species, it is therefore assumed that conditions are close to optimum for that species. It also has to be assumed that estimates of environment are close to accurate, and close to the optimum of the species, or else the species would not be so abundant.

Estimates of epilimnetic TP concentration for core samples were variable when planktonic species dominated the assemblages. For example, in Mariana Lake and again in Lake Wabamun (Seba core), variable TP concentrations were estimated when different planktonic species dominated the fossil samples. The planktonic species in the calibration lakes were more sensitive than the benthic species to variations in nutrient concentration. A strong relationship exists between planktonic species and water chemistry (Zhang & Prepas, 1996), and variation in dissolved nutrients results in planktonic species succession over the seasons (e.g., Round & Brooks, 1959; Hickman, 1979; Anderson, 1995; Moss *et al.*, 1997). Benthic species are associated with some kind of substrate instead of the water column, and low concentrations of TP were usually inferred when benthic species dominated the assemblages. Aquatic macrophytes take up phosphorus from the sediments and the water (Wetzel, 1975), and they can become a source of nutrients for some epiphytic algae (Wetzel, 1996). Epipelic species, found upon submersed sediments, can utilize the sediments as a nutrient source (Wetzel, 1983). When sediments are oxygenated, they are a sink for phosphorus (Wetzel, 1975). There is a poor correlation between periphyton (microscopic algae, bacteria and fungi on a substrate) and increased nutrients in the water column (Lowe, 1996). It is speculated that this is due to the compacted nature and steep resource gradients in the sediments (Lowe, 1996), and because epipelic species can remove sediment-related phosphorus for their own needs (Riber & Wetzel, 1987; Carlton & Wetzel, 1988). From this it can be inferred either that benthic diatom species are indifferent to nutrient concentrations in the water column, or that they are related to low nutrient concentrations in the water column for two reasons. They may be related to low epilimnetic nutrient concentration because of their ability to obtain nutrients from the sediments, or because planktonic species are poorly developed in water with low concentrations of nutrients resulting in little shading of the sediments. The latter situation can lead to a relatively clear water column and the potential of extensive benthic community development. It is probable that a weaker correlation exists between benthic species and epilimnetic TP concentration, and that a benthic-dominated assemblage may underestimate TP concentration. In many of the samples dominated by benthic species there were disagreements between inferences based on qualitative and quantitative data. Qualitative based inferences consider overall species ecology, plus other fossil evidence, whereas quantitative based inferences are made only on the reconstruction model.

The relationship between algal species and water chemistry can be confirmed in modern samples but not in fossil samples. In the upper most samples of the Cooking Lake core (20 - 0 cm), benthic species dominated. Diatom-inferred TP concentrations for these samples were low in comparison to diatom-inferred TP concentrations for previous samples in the core. Present day samples from the lake revealed that the planktonic community is dominant (as species of Chlorococcales and cyanobacteria), and the lake is hyper-eutrophic (Hickman, 1978, 1987). The benthic community in this lake is small. Planktonic algae other than diatoms dominate the modern flora, while benthic diatoms dominate the sedimentary record. In this lake there appears to be a very poor correlation between benthic diatom species and inferred TP concentration. When algae other than diatoms dominate the flora, an estimation of TP concentration is based on only a very small portion of the entire algal population. This situation can be confirmed with modern samples. By using sedimentary fossil pigments (as in the Lake Wabamun Moonlight Bay and Seba cores) the importance of other algal groups can be identified and these problems may be addressed for future lake core interpretations.

VI.F. Conclusions

1. Qualitative palaeolimnological methods provide descriptions of overall lake development, but results cannot be compared to modern lake measurements in a quantitative manner. Conversely, in theory quantitative methods can provide estimates of rates and magnitudes of changes, and thus comparisons to modern measurements can be made.
2. Inference models are derived from a set of data including modern lake chemical and physical parameters and diatom species assemblages. Often only one inference model is derived from these calibration data sets thus, only one variable is quantitatively reconstructed in palaeolimnological studies.
3. The model employed here to estimate TP concentration from sedimentary assemblages of diatoms should be used on lakes with modern measured TP concentration between 4 to 87 μg/l.

4. The reliability of TP concentration estimates is dependent upon the species assemblage in the sample and species distribution/relative abundance within the calibration data set. Species that occur in many lakes with similar concentration of TP have narrow optima, and fossil samples with high populations of these types of species will likely have reasonably accurate estimates of TP concentration.
5. Fossil samples containing unique species, or with populations of species found outside of the TP range of the calibration data set had unreasonable estimates of TP concentration.
6. In some lakes, or at certain times in the history of one lake, diatom assemblages may represent a very small proportion of the entire algal community. Estimates of TP concentration for these types of samples would likely be unreasonable or inaccurate.
7. In many samples, estimates of TP concentration were very likely underrepresented when assemblages were dominated by benthic species. Benthic species are either unrelated to dissolved TP concentration, or they are related to low concentrations of TP and light penetration (and subsequently small plankton population/high sediment illumination).
8. The best palaeolimnological studies should use multiple lines of evidence, quantitative and qualitative methods, together. The qualitative approach should employ multiple fossil groups such as diatoms, pigments, animals, pollen and plant macrofossils to provide information about the multiple components of the lake.

VI.G. References

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Table VI-1. Geographical positions and literature reference for the 8 lake cores used in the study. Oldest estimated date of each sediment core, the total length of each core and the lake water depth at the core site are given.

Lake Name	Reference	Latitude (°N)	Longitude (°W)	Oldest ^{14}C Date (years BP)	Core Length (cm)	Water Depth (m) (core site)
(A) Otasan	Chapter II	57° 42′	112° 23′	8220 +/- 110	320	7.5
(B) Mariana	Chapter III	55° 57′	112° 01′	11300 +/-110	709	6
(C) Spring	Hickman & White 1989	55° 31′	119° 35′	11200 +/-400	464	12.5
(D) Wabamun - Moonlight Bay	Hickman *et al.* 1984 and Hickman & Schweger 1991b	53° 35′	114° 26′	6600 (Mazama ash)	1067	2
(E) Wabamun - Seba	Hickman *et al.* 1984 and Hickman & Schweger 1991b	53° 30′	114° 44′	6600 (Mazama ash)	1554	10
(F) Fairfax	Hickman & Schweger 1991a	52° 58′	116° 34′	11255 +/-120	1000	5
(G) Goldeye	Hickman & Schweger 1993	52° 27′	116° 12′	> 14500	570	14
(H) Cooking	Hickman 1987	53° 26′	113° 02′	5220 +/-100	380	4

Table VI-2. Geographical positions and selected physical and chemical data for the 30 lakes used to derive the TP concentration inference model. Location of lakes are indicated in Figure VI-1.

Lake Number	Lake Name	Latitude (°N)	Longitude (°W)	Depth (m)	Area (km²)	TP (µg/l)	Magnesium (mg/l)	Calcium (mg/l)
5	L18	57° 26'	112° 37'	27.00	43.39	18.00	1.50	6.00
6	L19	57° 30'	112° 30'	10.50	7.25	36.00	4.00	16.00
7	L20	57° 32'	112° 29'	12.50	17.48	33.00	4.00	17.00
8	L21	57° 36'	112° 36'	13.00	17.17	65.00	3.50	11.00
9	L22	57° 42'	112° 22'	16.00	14.58	28.00	4.00	14.00
11	L25	57° 24'	112° 56'	9.40	16.76	42.00	1.00	3.00
21	L55	57° 13'	113° 02'	5.80	2.65	53.00	6.00	22.00
28	L62	57° 33'	112° 17'	6.00	1.48	83.00	8.00	27.00
30	L64	58° 08'	110° 47'	4.70	4.40	18.00	3.00	12.00
61	L104	54° 15'	119° 45'	11.00	0.54	12.00	10.00	34.00
63	L106	59° 42'	110° 21'	8.00	1.02	8.00	2.00	7.00
64	L107	59° 43'	110° 02'	14.10	2.72	4.00	1.00	6.00
66	L109	59° 07'	110° 49'	5.40	3.15	10.00	2.00	6.00
70	Mcleod	54° 18'	115° 39'	10.70	3.73	22.10	9.50	38.80
71	Long	54° 26'	112° 45'	28.00	1.62	62.50	17.80	22.30
72	Moose	54° 14'	110° 55'	19.80	40.80	39.00	44.60	22.90
73	Muriel	54° 08'	110° 41'	10.70	64.10	32.00	115.00	7.00
74	Tucker	54° 32'	110° 36'	7.50	6.65	49.00	34.00	16.00
75	Bonnie	54° 09'	111° 52'	6.10	3.77	41.00	43.00	31.00
76	Buck	53° 00'	114° 45'	12.20	25.40	61.00	6.00	23.30
77	Crimson	52° 27'	115° 02'	9.10	2.32	17.40	18.00	21.30
79	Wabamun	53° 33'	114° 36'	11.00	81.80	36.30	14.90	22.60
80	Pigeon	53° 01'	114° 02'	9.10	96.70	33.00	11.60	26.00
81	Dillberry	52° 35'	110° 00'	10.70	0.80	16.80	27.30	22.30
83	Gull	52° 34'	114° 00'	8.00	80.60	49.00	64.50	12.30
84	Sylvan	52° 18'	114° 06'	18.30	42.80	20.00	36.00	17.60
86	Coal	53° 08'	113° 21'	5.50	10.90	72.90	12.00	
87	Sturgeon	55° 06'	117° 32'	9.50	49.10	62.30	5.50	21.30
89	Crooked	54° 55'	113° 33'	8.50	1.09	65.00	13.88	33.20
93	Pine	52° 04'	113° 27'	12.20	3.89	87.00	24.50	26.40
	Minimum			4.70	0.54	4.00	1.00	3.00
	Maximum			28.00	96.70	87.00	115.00	38.80
	Mean			11.34	21.62	39.21	18.27	18.80
	Median			10.60	6.95	36.15	9.75	21.30
	SD			5.70	27.83	22.92	24.05	9.40

Table VI-3. Summary of data from 6 climate stations in Alberta (Atmospheric Environment Service, 1993). Location of stations indicated on Figure VI-1.

Station	Latitude (°N)	Longitude (°W)	Annual Mean Temperature (°C)	Total Precipitation (mm)	No. Days Maximum Temperature more than 0 °C	Total July Precipitation (mm)	Daily Mean July Temperature (°C)
(I) Red Deer	$52^{\circ} 11^{1}$	$113^{\circ} 54^{1}$	2.3	470.2	274	87.9	15.8
(J) Edmonton	$53^{\circ} 18^{1}$	$113^{\circ} 35^{1}$	2.1	465.8	269	101.0	16.0
(K) Ft. McMurray	$56^{\circ} 39^{1}$	$111^{\circ} 13^{1}$	0.2	464.7	245	79.1	16.6
(L) Grand Prairie	$55^{\circ} 11^{1}$	$118^{\circ} 53^{1}$	1.6	450.2	266	67.9	16.0
(M) Buffalo	$57^{\circ} 57^{1}$	$116^{\circ} 13^{1}$				106.8	14.4
(N) Whitesand	$59^{\circ} 26^{1}$	$114^{\circ} 54^{1}$				70.3	12.5

Table VI-4. Species names (and corresponding numbers) used in Canonical Correspondence Analysis and the weighted-averaging regression and calibration TP inference model. Species are listed by estimated TP optimum. Also given are total number of occurrences and maximum relative percent abundance in the 30 calibration lakes.

		TP	No.	Max.
Number	Species Name and authority	$\mu g\ l^{-1}$	Occur.	Abun.
14	*Anomoeoneis serians* (Brébisson) Cleve	4.00	1	1
41	*Cymbella gracilis* (Ehrenberg) Kützing	4.00	1	1
115	*Navicula laevissima* Kützing	4.00	1	1
36	*Cyclotella tripartita* Håkansson	4.63	2	16
31	*Cyclotella hakanssoniae* Wendker	5.23	2	11
6	*Achnanthes linearis* (W. Smith) Grunow	5.72	2	1
156	*Tabellaria flocculosa* (Roth) Kützing strain IV sensu Koppen	6.43	2	2
44	*Cymbella ventricosa* Kützing	8.03	1	1
87	*Fragilaria vaucheriae* (Kützing) Petersen	8.03	1	1
119	*Navicula pseudoscutiformis* Hustedt	8.03	1	1
133	*Nitzschii fonticola* Grunow	8.33	3	2
88	*Fragilaria virescens* Ralfs	9.40	2	6
39	*Cymbella cesatii* (Rabenhorst) Grunow	9.53	2	4
8	*Achnanthes peragalli* Brun & Heribaud	10.02	1	1
23	*Aulacoseira lirata* (Ehrenberg) Ross	10.02	1	1
109	*Navicula halophila* (Grunow) Cleve	10.02	1	1
111	*N. jaernefeltii* Hustedt	10.02	1	3
146	*Pinnularia viridis* (Nitzsch) Ehrenberg	10.02	1	1
42	*Cymbella microcephala* Grunow	10.12	5	4
148	*Stauroneis anceps* Ehrenberg	10.94	2	1
16	*Anomoeoneis vitrea* (Grunow) Ross	11.68	2	1
53	*Epithemia zebra* (Ehrenberg) Kützing	11.94	1	1
97	*Gomphonema parvulum* (Kützing) Kützing	11.94	1	1
147	*Rhopalodia gibba* (Ehrenberg) O.Müller	11.94	1	1
7	*Achnanthes minutissima* Kützing	12.54	7	2
122	*Navicula radiosa* Kützing	13.01	3	1
20	*Aulacoseira distans* (Ehrenberg) Simonsen	13.59	2	11
9	*Achnanthes suchlandtii* Hustedt	14.10	4	3
121	*Navicula pupula* Kützing	15.69	4	1
28	*Cocconeis neodiminuta* Krammer	16.81	1	1
91	*Gomphonema angustissima* Agardh	16.81	1	3
120	*Navicula pseudoventralis* Hustedt	16.81	1	1
105	*N. cryptotenella* Lange-Bertalot	17.17	2	7
30	*Cyclotella distinguenda* Hustedt	17.65	4	26
27	*Cocconeis disculus* (Schumann) Cleve	18.20	3	2
157	*Tabellaria flocculosa* (Roth) Kützing strain IIIp sensu Koppen	19.57	9	21
81	*Fragilaria leptostauron v. martyi* (Heribaud) Lange-Bertalot	19.99	10	9
33	*Cyclotella pseudostelligera* Hustedt	20.05	8	29
34	*C. radiosa* (Grunow) Lemmermann	20.61	12	12

Table VI-4. Continued.

2	*Achanthes exigua* Grunow	20.76	3	2
35	*Cyclotella stelligera* Cleve & Grunow	21.47	9	19
74	*Fragilaria construens v. construens* (Ehrenberg) Grunow	23.26	19	23
4	*Achnanthes lanceolata* (Brébisson) Grunow	25.05	12	5
32	*Cyclotella meneghiniana* Kützing	25.66	2	6
137	*Nitzschii paleacea* Grunow	26.80	2	3
76	*Fragilaria construens v. venter* (Ehrenberg) Hustedt	26.99	21	22
85	*Fragilaria pinnata* Ehrenberg	28.49	25	30
162	*Navicula* cf. *submuralis* Hustedt	30.06	3	3
12	*Amphora libyca* Ehrenberg	30.69	8	4
69	*Fragilaria brevistriata* Grunow	32.02	22	82
136	*Nitzschii palea* (Kützing) W.Smith	33.12	1	2
160	*Navicula* cf. *mediocris* Krasske	34.34	2	1
1	*Achnanthes conspicua* Mayer	35.13	2	1
132	*Nitzschii amphibia* Grunow	35.71	3	1
13	*Amphora pediculus* (Kützing) Grunow	35.82	17	9
123	*Navicula recens* (Lange-Bertalot) Lange-Bertalot	35.97	1	1
125	*N. seminulum* Grunow	35.97	1	2
17	*Asterionella formosa* Hassall	37.05	18	16
22	*Aulacoseira italica* (Ehrenberg) Simonsen	39.33	4	23
70	*Fragilaria capucina* Desmazièrs	39.33	11	22
77	*F. crotonensis* Kitton	39.69	16	30
96	*Gomphnema minutum* (Agardh) Agardh	40.69	4	2
82	*Fragilaria nanana* Lange-Bertalot	41.22	3	13
29	*Cocconeis placentula* Ehrenberg	41.99	6	2
153	*Stephanodiscus parvus* Stoermer & Håkansson	42.64	22	59
21	*Aulacoseira granulata* (Ehrenberg) Simonsen	42.90	14	55
19	*Aulacoseira ambigua* (Grunow) Simonsen	43.39	16	31
152	*Stephanodiscus niagarae* Ehrenberg	47.86	22	41
151	*Stephanodiscus hantzschii* Grunow	50.94	2	4
78	*Fragilaria elliptica* Schumann	82.93	1	1
71	*F. capucina v mesolepta* (Rabenhorst) Rabenhorst	87.23	1	3

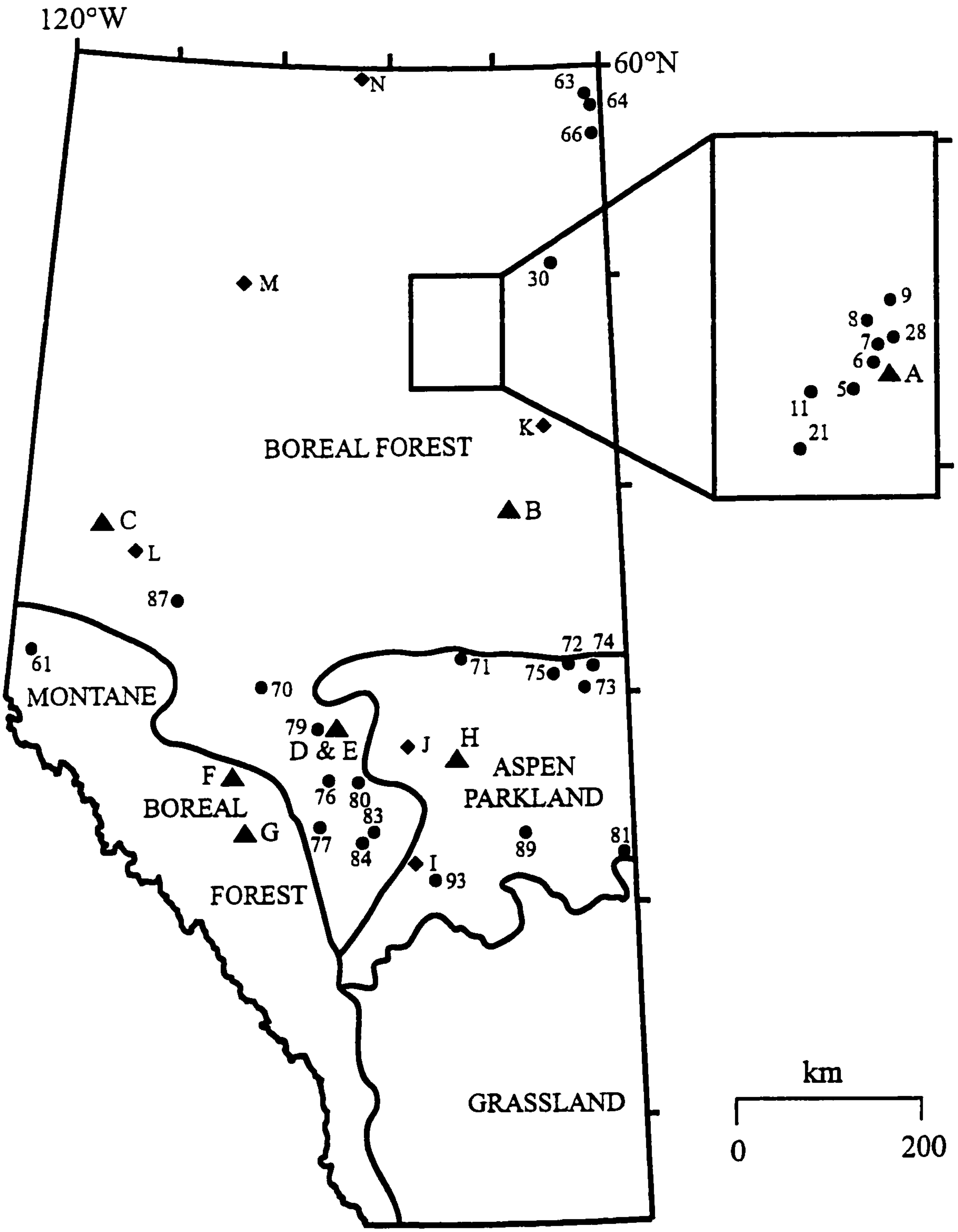

Figure VI-1. Map of Alberta indicating the location of the 30 lakes (●), 8 coring sites (▲) and 6 climate stations (◆).

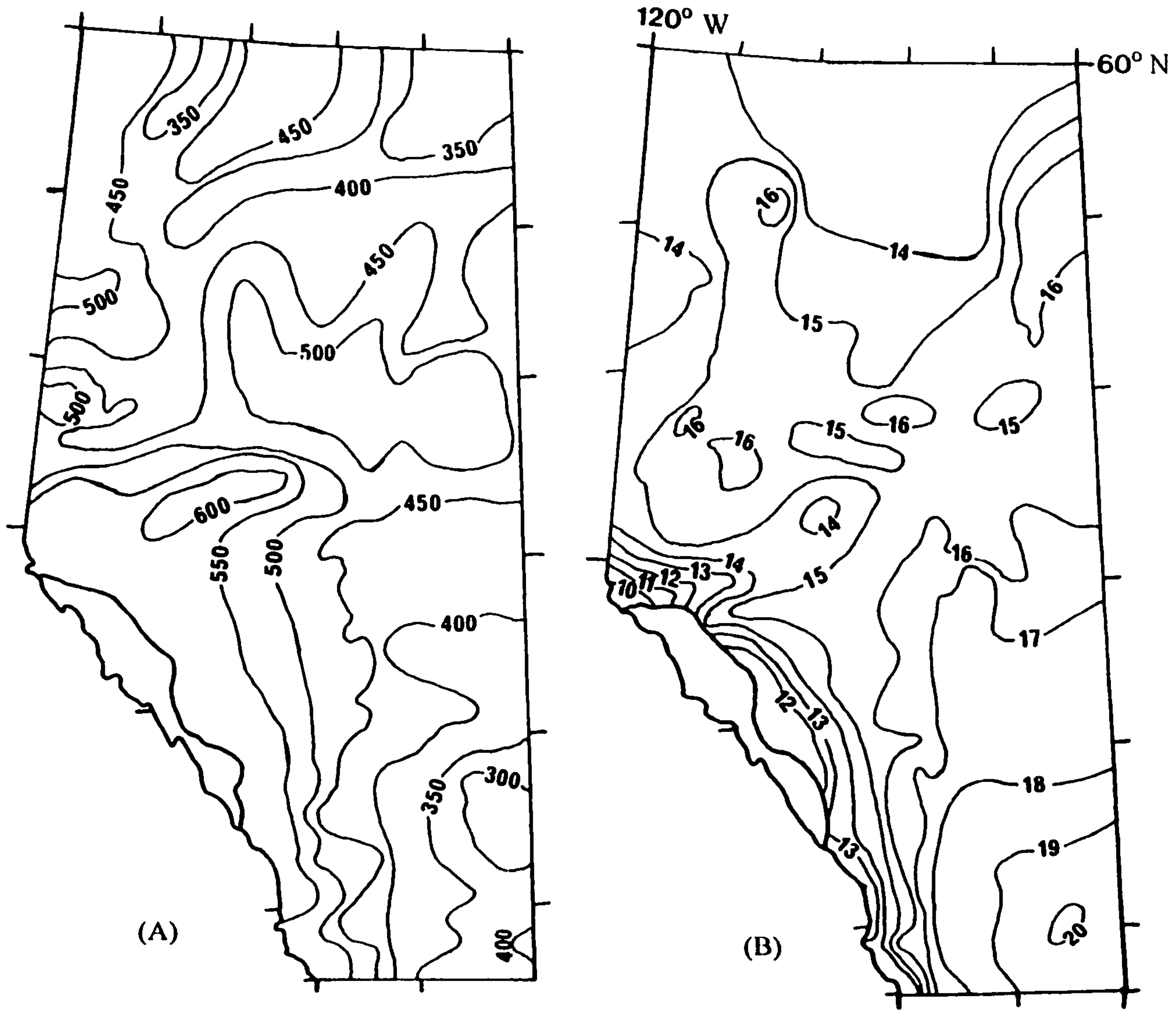

Figure VI-2. General climate of Alberta as summarized by (A) total annual precipitation (mm) and (B) mean July temperature (degree C). Modified from Atlas of Alberta (1984).

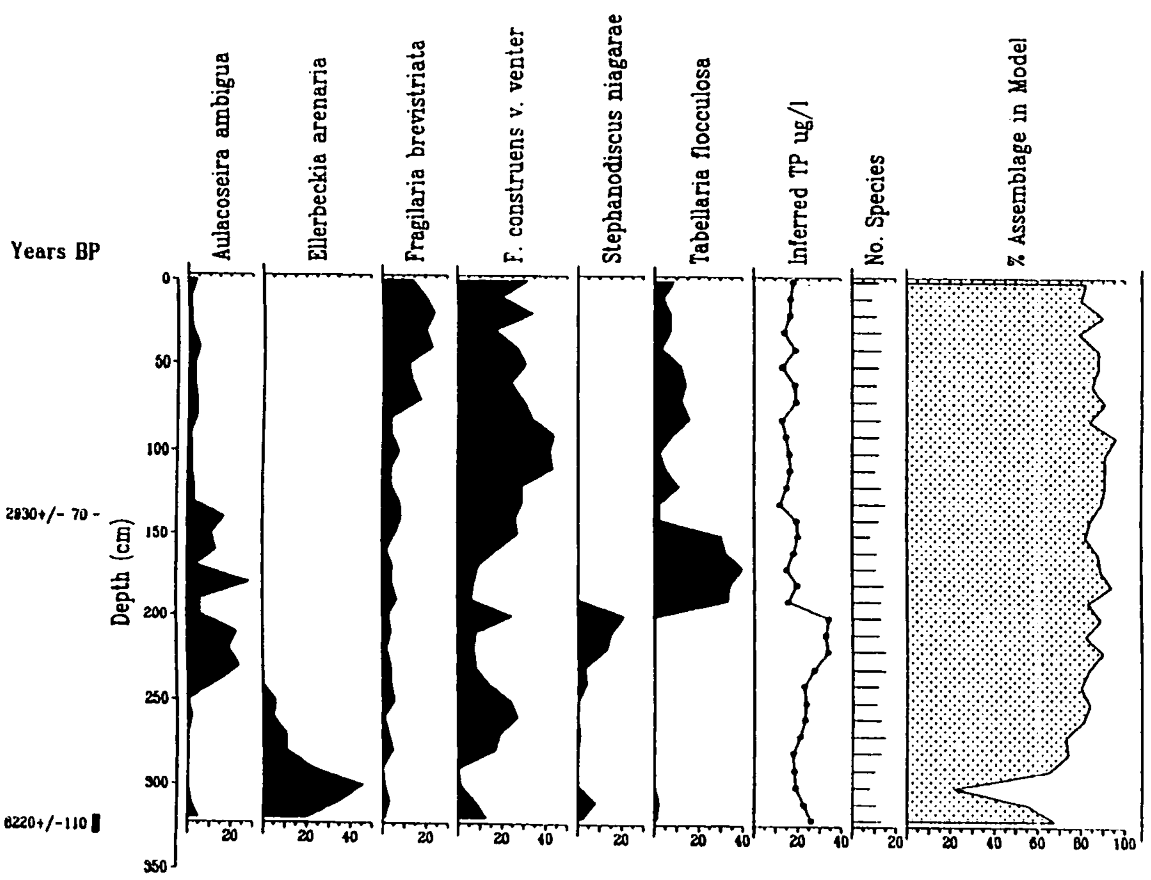

Figure VI-3. Summarized diatom stratigraphy and inferred TP concentration (ug/l) for Otasan Lake. Also indicated are the number of species and percent of the total assemblage used in the model. All samples had modern analogues.

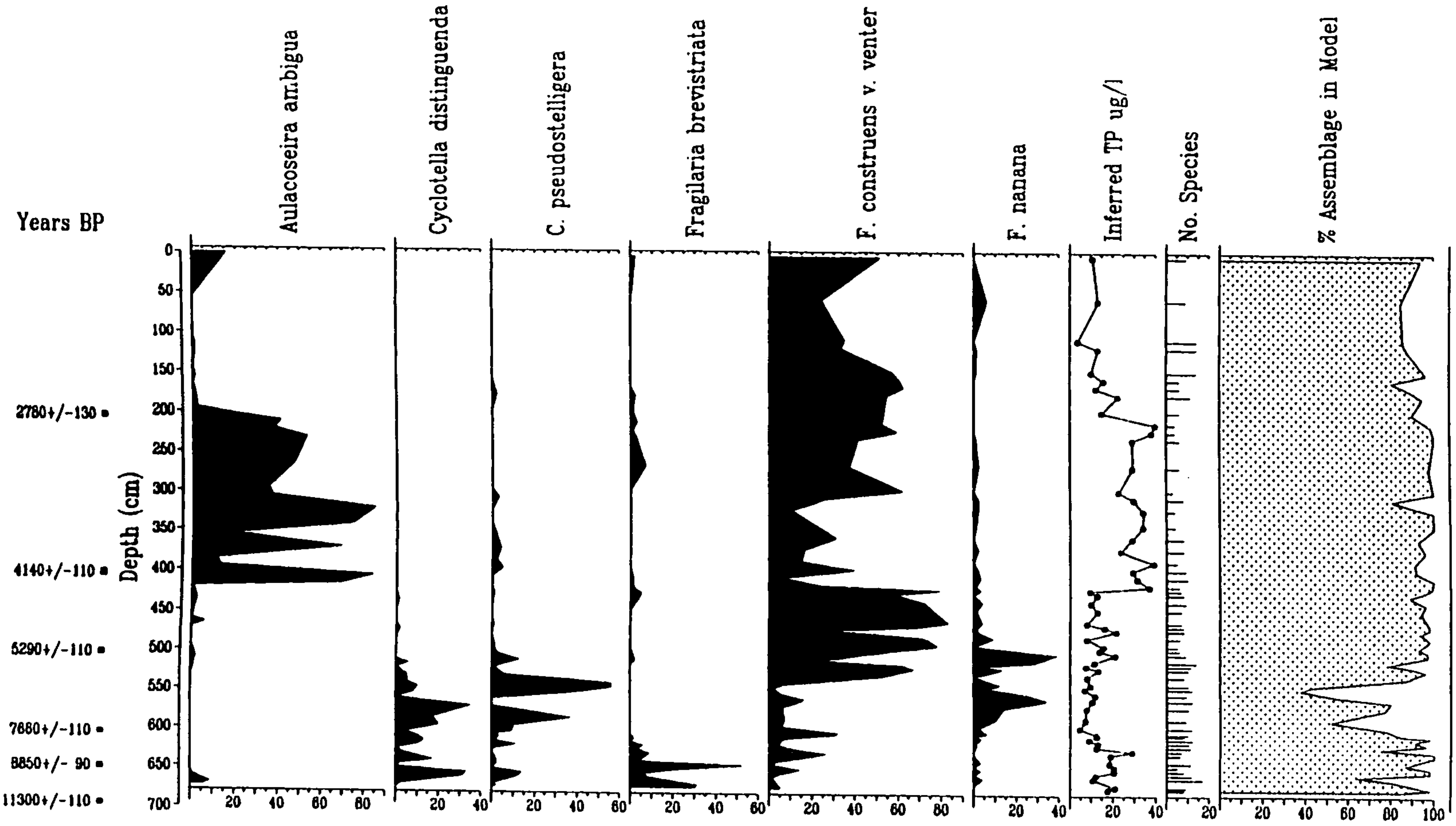

Figure VI-4. Summarized diatom stratigraphy and inferred TP concentration (ug/l) for Mariana Lake. Also indicated are the number of species used and percent of the total assemblage used in the model. All samples had modern analogues.

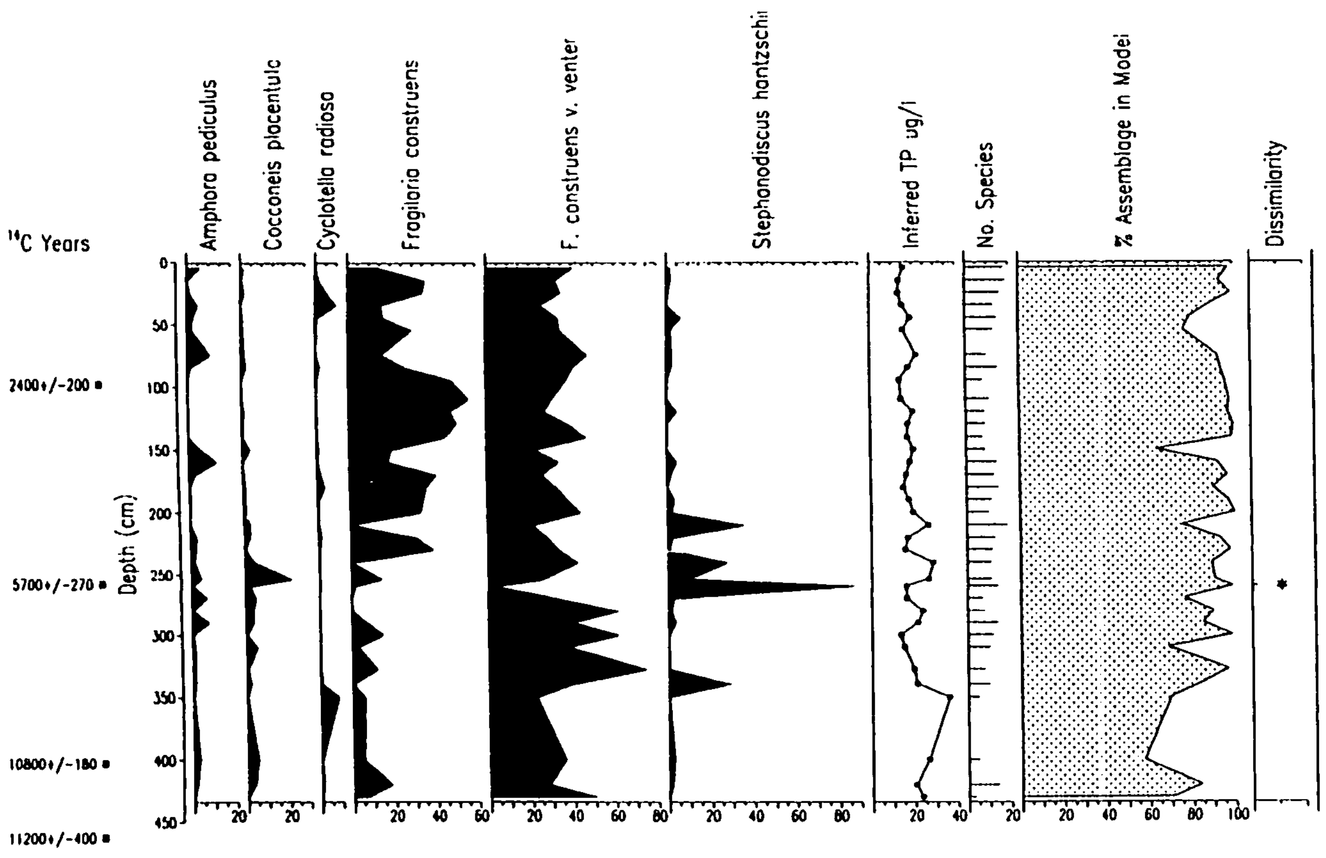

Figure VI-5. Summarized diatom stratigraphy and inferred TP concentration (µg/l) for Spring Lake. Also indicated are the number of species and percent of total assemblage used in the model. (* indicates assemblage significantly different than modern assemblages)

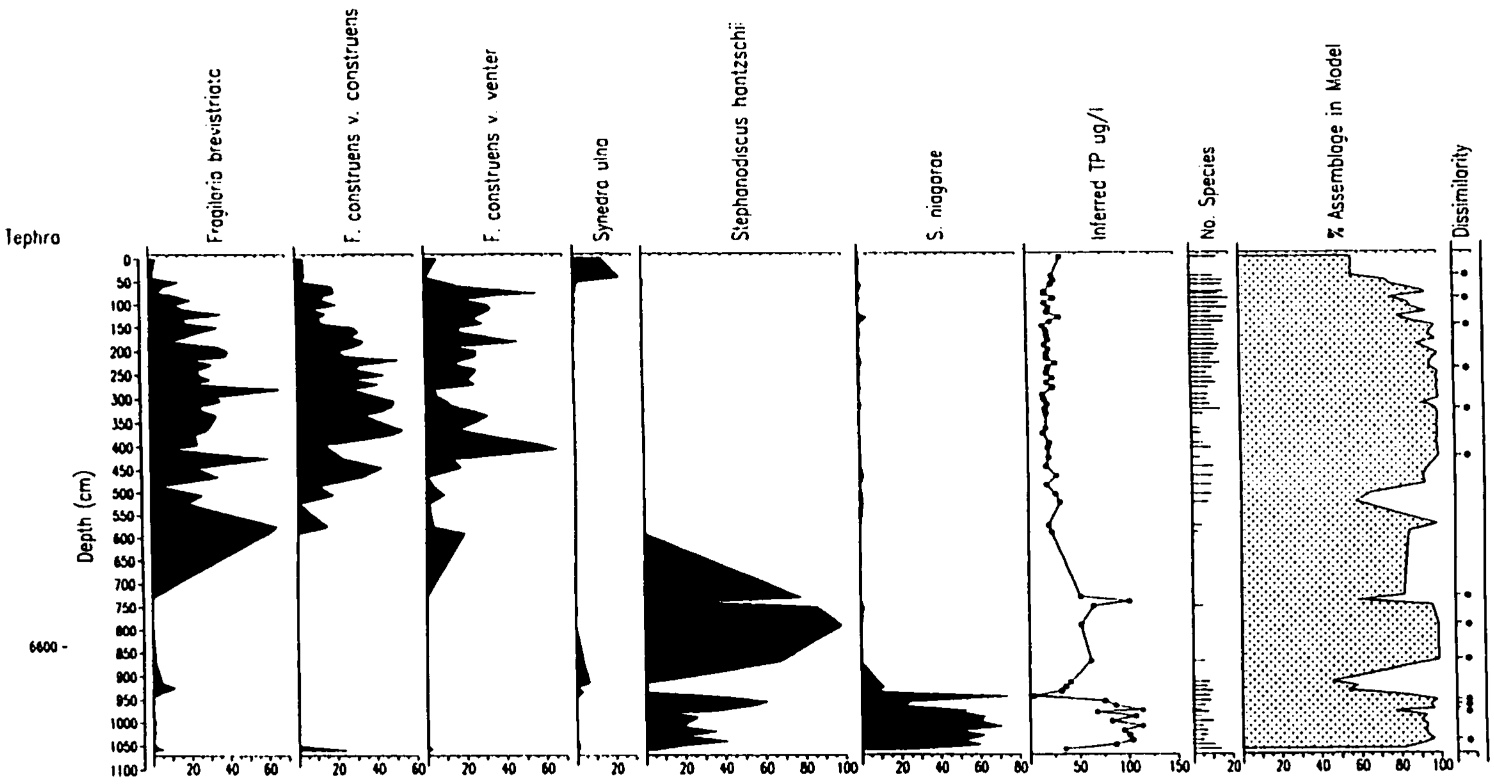

Figure VI-6. Summarized diatom stratigraphy and inferred TP concentration (µg/l) for Moonlight Bay (Lake Wabamun). Also indicated are the number of species and percent of the total assemblage used in the model. (* indicates assemblage significantly different than modern assemblages)

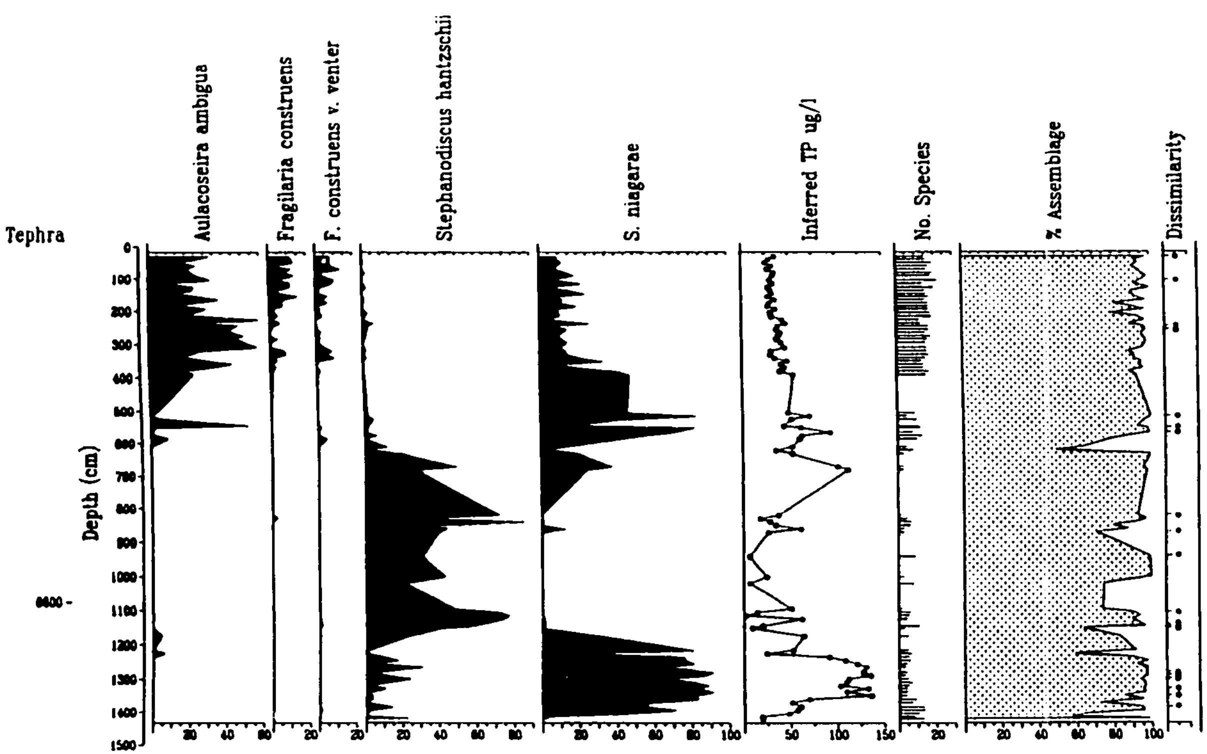

Figure VI-7. Summarized diatom stratigraphy and inferred TP concentration (μg/l) for Seba (Lake Wabamun). Also indicated are the number of species and percent of the total assemblage used in the model. (* indicates assemblage significantly different than modern assemblages)

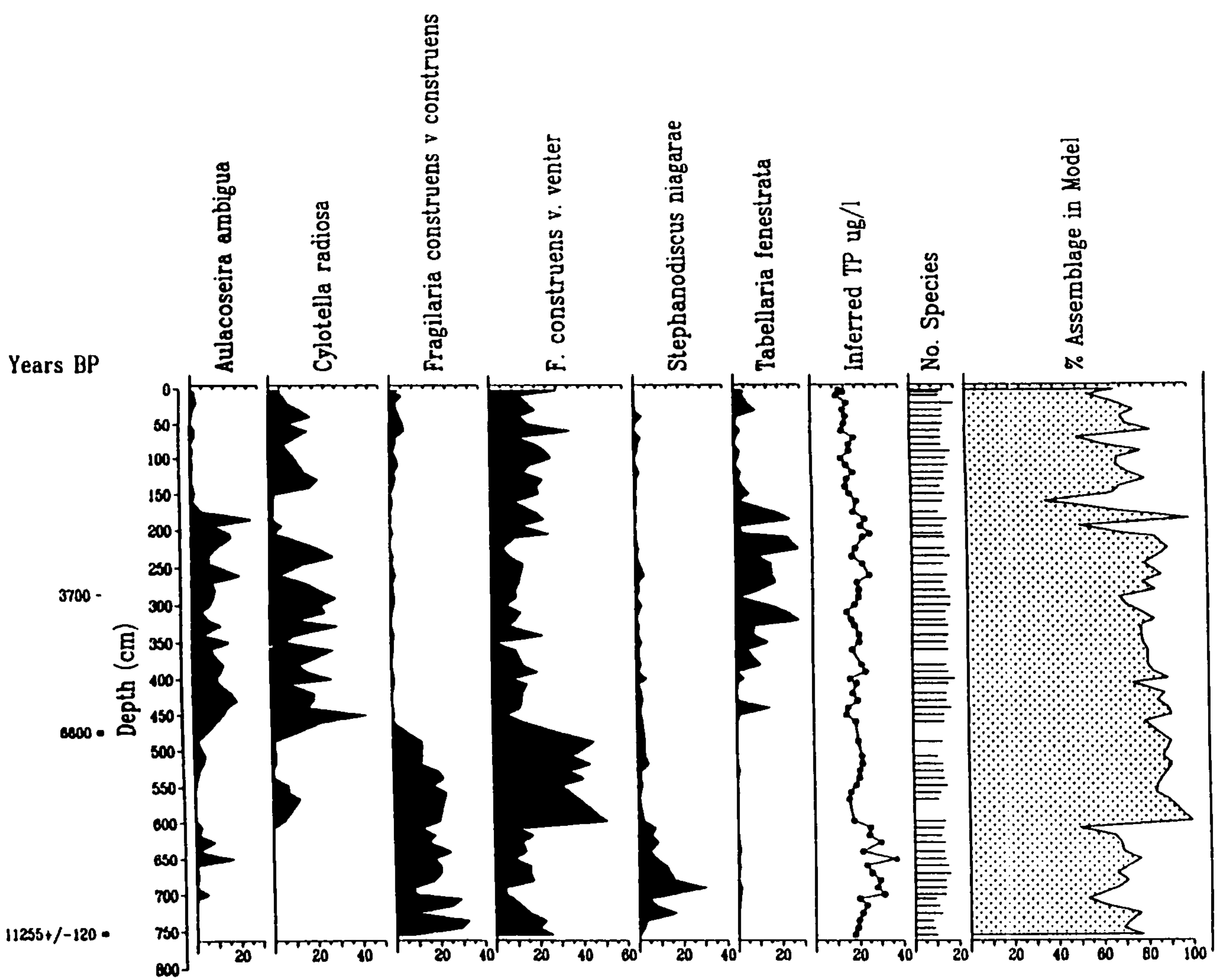

Figure VI-8. Summarized diatom stratigraphy and inferred TP concentration (µg/l) for Fairfax Lake. Also indicated are the number of species and percent of total assemblage used in the model. All samples had modern analogues.

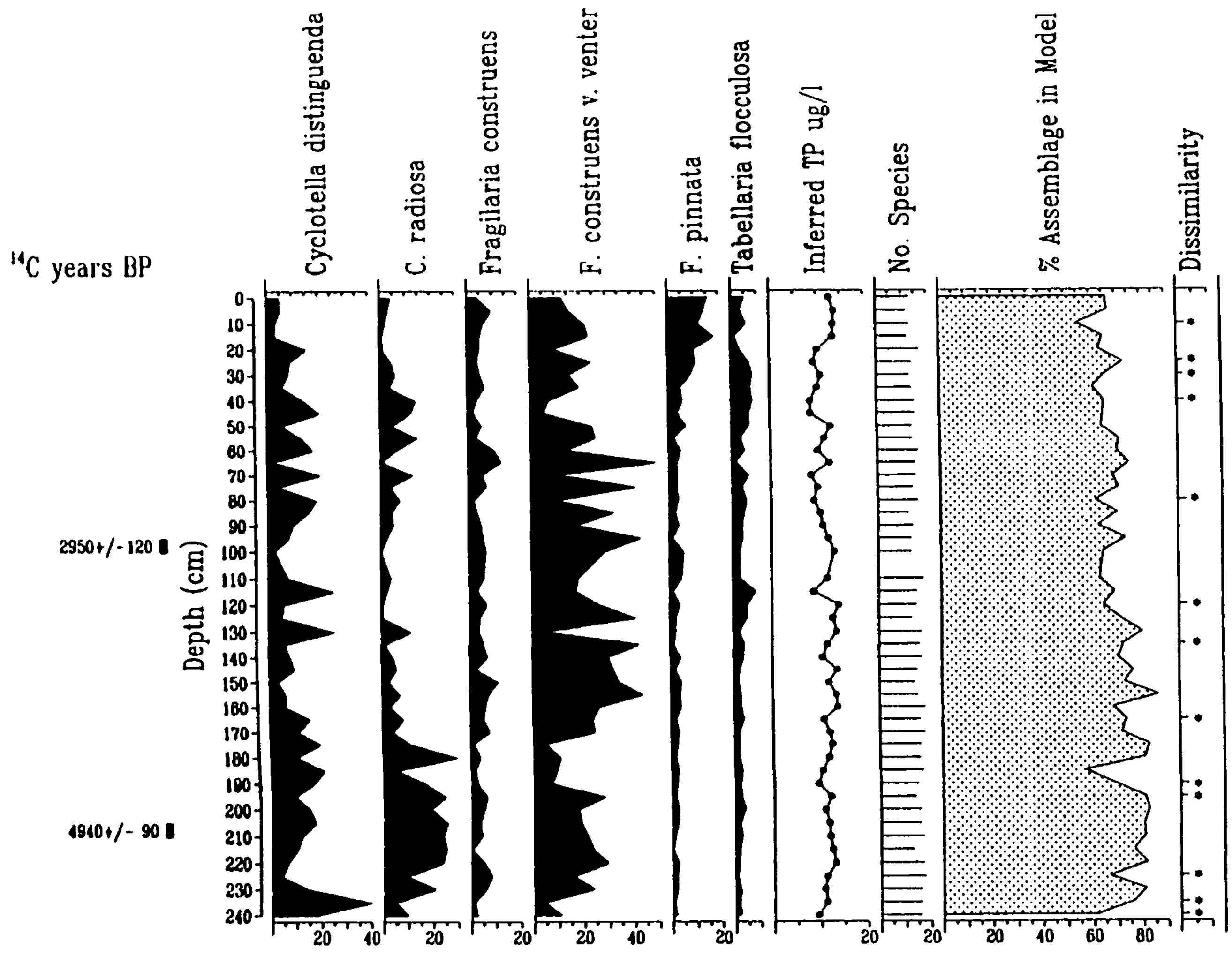

Figure VI-9. Summarized diatom stratigraphy and inferred TP concentration (μg/l) for Goldeye Lake. Also indicated are the number of species and the percent of the assemblage used in the model. (* indicates assemblage significantly different than modern assemblages)

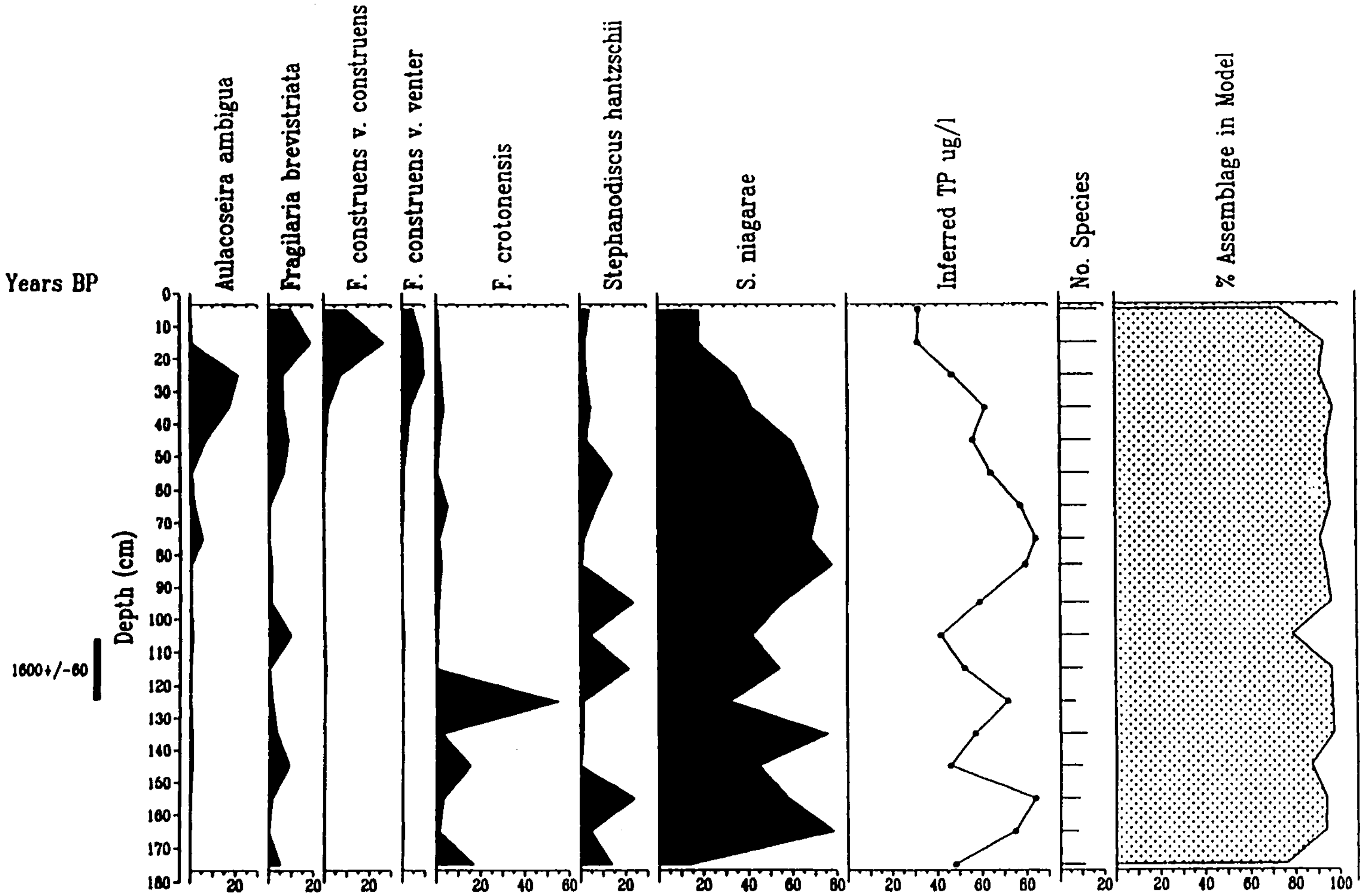

Figure VI-10. Summarized diatom stratigraphy and inferred TP concentration (µg/l) for Cooking Lake. Also indicated are the number of species and percent of the total assemblage used in the model. All samples had modern analogues.

Chapter VII. A synthesis of modern and fossil diatom assemblages and ecological and palaeoecological inferences.

Assemblages of diatom species (Bacillariophyceae) from both surficial and fossil lake sediment samples were analyzed. The lakes selected for study are located in the Boreal Forest, Montane Boreal Forest and the Aspen Parkland ecoregions of Alberta (Strong & Leggat, 1981). Diatoms are used in palaeolimnological studies because they preserve well in accumulating sediments, they are easily extracted from organic sediments (unlike soft bodied algae) and they are influenced by physical and chemical lake variables (Anderson *et al.*, 1986). In addition, each diatom fossil represents a half to a whole organism thus making estimations of populations and communities more realistic. Diatoms are widely used in ecological studies of lakes because they are found in all lentic (still water) habitats (Round, 1981), they are usually very abundant in those habitats, and they are significantly related to many environmental variables in the aquatic ecosystem (e.g., Hustedt, 1937-39; Round, 1957a, 1957b; Meriläinen, 1967; Charles, 1985; Agbeti & Dickman, 1989; Birks *et al.*, 1990; Reavie *et al.*, 1995).

Long sediment records from two lakes in northern Alberta were studied (Otasan Lake and Mariana Lake) because long-term studies of lakes from this region are lacking (Chapter II & III). The record from Otasan Lake spanned *ca.* 8200 years, the fossil diatom assemblages changed over this period and interpretations were made from these changes (Chapter II). The younger basal date (in light of older age estimates for deglaciation [Dyke & Prest, 1987]), and the absence of a "typical" pioneering flora (*Ellerbeckia arenaria* initial diatom species) suggest that this was not a complete fossil record. It was hypothesized that the expansion of the peatlands in the catchment was responsible for the present day slightly acidic lake water. The development of a large acidophilic diatom assemblage between *ca.* 5000 to 3100 years BP indicated that the peatlands acidified the lake (to pH 5.5 to 6), but after *ca.* 3100 years BP the lake recovered to approximately pH 6.5. The recovery in pH was possibly because of less evaporation stress and more precipitation (Vance, 1986b), and permafrost development (Zoltai, 1993) within the catchment after *ca.* 3100 years BP. It was also hypothesized that the diatom record would be more sensitive than the pollen record to climate changes (precipitation, temperature, evaporation). The pollen record from a lake within the vicinity of Otasan Lake indicated that little change had occurred in the vegetation since *ca.* 7500 years BP (Vance, 1986a). The Otasan Lake diatom record indicated that lake productivity was high and the lake was eutrophic between *ca.* 7300 to 5000 years BP (due to climate), then acidic (due to peatland expansion) and has only been "stable" since *ca.* 3100 years BP. Algae and some other aquatic organisms are more sensitive than vegetation to slight changes in the environment because of their short life spans.

The basal date from the Mariana Lake core was 11,300 ± 110 years BP (Chapter III). The earliest samples for diatom analysis (*ca.* 9100 years BP) contained an assemblage of benthic *Fragilaria* and small *Cyclotella* species. This was also not a "typical" pioneering flora, but samples from the first 100 cm of the core were not available for this study. The objectives of the Mariana Lake study were to compare fossil pollen (Hutton *et al.*, 1994), peatland (Nicholson & Vitt, 1990) and diatom records and the response of the organisms to inferred increased mid-Holocene aridity. In addition, effects of changing climate on lakes to the north and south were discussed in comparison to Mariana Lake.

Peatland development did not significantly impact Mariana Lake, but the Holocene thermal optimum did influence its development. The Holocene thermal optimum is estimated to have occurred between *ca.* 8000 to 7000 years BP from the peatland record (Nicholson & Vitt, 1990), between *ca.* 7500 to 5500 years BP from the pollen record (Hutton *et al.*, 1994) and between *ca.* 7500 to 4300 years BP from the diatom record. The data suggested that the climatic optimum had a longer lasting effect on the lake biota than on the catchment vegetation. As inferred from the diatom record, the lake was initially deep but unproductive (a consequence of poor mixing of the water column and sediments), and then it was shallow (a lag effect of warm climate by decreasing water tables) between *ca.* 9100 to 4300 years BP. In the initial phase of this diatom zone, Otasan Lake was very productive (Chapter II), while lakes to the south were saline (Hickman & Schweger, 1996) or empty (Hickman *et al.*, 1990). Mariana Lake was most productive between *ca.* 4300 to 2700 years BP. Otasan Lake was acidic during the same time period, due to peatland encroachment towards the modern lake margin, while lakes with currently deep basins were becoming less saline (Hickman & Schweger, 1996) and most presently shallow lake basins were beginning to fill (Schweger & Hickman, 1989).

It appears that most vegetation patterns in Alberta have been relatively stable since *ca.* 3000 years BP (e.g., Hickman *et al.*, 1984; McDonald & Reid, 1989; Hutton *et al.*, 1994). Some lake records indicate that lakes have also been relatively stable over the same time period (possibly more a reflection of an insensitive flora), while some lakes have only been relatively stable since the last 1000 years due to slight changes in their catchment, and the response of a sensitive terrestrial/aquatic flora to fire.

Lakes and ponds are abundant in northern Alberta, yet the biological composition of many of them is unknown. It is known that diatoms are influenced by environmental conditions. Consequently, an investigation into the relationship between diatom species assemblages and lake chemical and physical variables in lakes from northern to central Alberta was undertaken (Chapter IV). Surficial sediments are assumed to contain a spatial and temporal mixture of recent diatom assemblages (Dixit *et al.*, 1995) so surficial sediments from 93 lakes were retrieved. The first objective, to analyze diatom diversity, resulted in the identification of 209 diatom species. In future the taxonomy of these diatoms and associated problems with diatom nomenclature will be discussed.

The second objective was to analyze the relationship between these species and measured lake variables. A number of statistical steps were followed to analyze these relationships. Water depth was found to be the most important variable because it separated ponds or wetlands from larger lakes on the basis of dominant algal community. Planktonic species typically dominated in deeper lakes, while benthic species typically dominated in shallow ponds. Within the two lake groups, variations in water chemistry (the concentration of total phosphorus (TP), magnesium and bicarbonate) were evident. Diatom calibration data sets are commonly generated for a specific variable such as pH (e.g., Birks *et al.*, 1990), TP (e.g., Reavie *et al.*, 1995), dissolved organic carbon (e.g., Pienitz & Smol, 1993) and salinity (e.g., Wilson *et al.*, 1996). The lakes in this study were chosen to represent lentic water bodies in Alberta and not to follow a predefined environmental gradient. It was hypothesized that significant relationships between diatoms and environmental gradients would still be evident in a random collection of lakes. Water depth and variables related to water chemistry significantly influenced the distribution of diatom species in these lakes. Water depth is important because of its influence upon algal community. The importance of water depth in calibration data sets decreases as the depth range decreases (Fritz *et al.*, 1993) or as the range in other variables increases (Reavie *et al.*, 1995). Many lakes in Alberta have high concentration of hard water ions (magnesium, calcium, bicarbonate, carbonate, sulphate, potassium and sodium) (Wetzel, 1975) and they apparently are important in influencing the distribution of diatom species.

Many of the shallow ponds and wetlands from this study (Chapter IV) were from northern Alberta. These results indicated that the ponds within northern Alberta and within smaller regions of northern Alberta are quite different from each other, both chemically and biologically, possibly due to variations between catchments (Hall & Smol, 1993). These regions are currently primarily disturbed by forestry and gas exploration (Bailey, 1989; Forestry, Lands & Wildlife, 1992; Alberta-Pacific, 1994), yet the effect of such practices on the aquatic ecosystem is poorly studied. Many species were restricted to a small number of these ponds, suggesting that northern Alberta may have unique ecosystems, or that species are very sensitive to small differences.

A subset of lakes from the large data set was used to derive a statistical inference model (Chapter V). The deeper lakes had a better relationship to water chemistry and so only they were used in this portion of the study. Lakes deeper than 3.5 m were retained, but no other requirement was defined. The first objective was to determine if any water chemistry variables were significantly related to diatom species distribution in these lakes, and it was hypothesized that significant relationships would be determined even without selecting lakes to fit along a predefined gradient. Concentration of total phosphorus (TP), magnesium and calcium along with lake area significantly influenced the distribution of diatom species across these lakes. Some diatom species clearly preferred oligotrophic, soft water lakes, while other species preferred eutrophic, hard water lakes. Some species were more sensitive to the TP concentration gradient, while others were more sensitive to the dissolved magnesium ion gradient. It was also hypothesized that the relationship between diatom species in Alberta lakes would be different from the relationship between diatom species in other lakes. This would limit the usefulness of inference models between areas. The importance of the gradient of water hardness in these lakes suggested that ecological relationships might differ between regions. Future studies could explore in more detail these ecological associations and the relationship between TP concentration, water hardness and diatom or total algal production in lakes. The final objective was to derive a statistical inference model from this data set. A model to infer TP concentration of the water from sedimentary diatom assemblages was derived. The variable TP was chosen because it was the most important variable in this smaller data set of lakes, and it is ecologically important since it often limits biological productivity (Wetzel, 1975). It was shown that the model can be used to infer TP concentration between 4 and 87 μg TP/l. This model should only be used on Alberta lakes due to underlying influences that may be similar among most Alberta lakes. Finally, this model may be of use to lake managers in determining lake nutrient budgets.

The TP concentration inference model derived in Chapter V was applied to the post-glacial sedimentary record from seven Alberta lakes (Chapter VI). The optimum TP concentration for each diatom species in the local calibration data set was estimated. By using the regression model, TP concentration was estimated for each fossil sample, based on the relative percent abundance of each species in the sample and the estimated TP concentration optima of all species. The application and limitation of inference models in general was discussed. The first objective was to apply the model to eight lake cores (from seven lakes) to assess the usefulness of the model. The inference model was used on the cores from Otasan Lake (Chapter II), Mariana Lake (Chapter III), Spring Lake (Hickman & White, 1989), Lake Wabamun (Moonlight Bay and Seba) (Hickman *et al.*, 1984; Hickman & Schweger, 1991b), Fairfax Lake (Hickman & Schweger, 1991a), Goldeye Lake (Hickman & Schweger, 1993) and Cooking Lake (Hickman, 1987).

Second, since all cores had been previously described by qualitative methods, a comparison to quantitative methods was also made. It was determined that the best palaeoecological studies should use a variety of organisms and methods to describe and document the development of the lake. The third objective was to discuss limitations of quantitative inference models. Reliable sample estimates are derived if fossil species are also found in the modern samples (and estimates of species TP concentration are derived for them), if the relative percent abundance of individual species is similar in fossil and modern samples, and if fossil species assemblages are analogous to modern species assemblages. The final objective was to determine if quantitative palaeolimnological methods could be used on all lake records. If diatom communities do not represent a large proportion of the total algal assemblage, if fossil samples contain very few species, and sometimes if the benthic diatom community is dominant, then very poor estimates of the variable are derived. Benthic diatom communities often dominate in lake records, yet often the relationship between benthic species and water chemistry is poor. It is suggested that inference models based on benthic species should be derived, and applied to sections of sediment cores where the benthic community dominates.

This study has illustrated the usefulness of diatoms in both ecological and palaeoecological studies. From the analysis of modern samples, the biological diversity of diatoms in Alberta was investigated. It was shown that water depth is a prime determinant of dominant algal community. It was then determined that concentrations of magnesium, bicarbonate and calcium (water hardness), as well as TP concentration, are important in Alberta lakes. Diatom species respond primarily to those variables of water chemistry. It was shown that the planktonic species had a better relationship to water chemistry than the benthic species. An investigation into the relationship between epipelic diatoms and chemistry of the water immediately overlying the sediments should be done. This would provide information on the epipelic community and could lead into studies on the importance of the epipelon in the lake ecosystem. This study indicated that lakes within northern Boreal regions have developed overtime, and that each lake record can potentially provide information on this ecoregion. The large diatom data base provided biological and chemical data from a wide range of lakes in northern and central Alberta. It represents a base for further study on these aquatic ecosystems.

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