ASSESSING THE IMPACT OF ANTHROPOGENIC DISTURBANCES ON WATER QUALITY IN CANADIAN SHIELD LAKES: A PALEOLIMNOLOGICAL PERSPECTIVE

by

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For my brother Stuart..."A ray of sunshine only lent"

ABSTRACT

Historically remote, Canadian Shield lakes situated in boreal and mixed-boreal regions have become increasingly threatened by anthropogenic disturbances. Due to a scarcity of long-term data, the effects of these disturbances on water quality are poorly understood. In this thesis, I applied paleolimnological techniques to examine the impact of watershed and regional-scale disturbances on the water quality of Canadian Shield lakes in Ontario, Canada.

Scaled chrysophytes preserved in lake sediments were examined to assess the impact of logging and forest fires on water quality. A 'Before-After-Control-Impact' design, including six impact lakes (4 with watersheds logged, 2 with watersheds burned), and two reference lakes in northwestern Ontario was implemented. Despite removal of more than 90% of the vegetation of the disturbance lakes, neither logging nor forest fires produced significant changes in chrysophyte-inferred water quality. Subtle, gradual species changes, occurring in both disturbance and reference lakes, suggested that a regional, prolonged drought may have been responsible for the observed changes in these lakes.

The impact of acid deposition on changes in lakewater pH was examined in 53 present-day (top) and 48 pre-industrial (bottom) sediment samples from shield lakes in south-central Ontario. A 117-lake reconstruction model, developed from a training set of lakes in Ontario, Adirondack Park, and the northeastern USA, was used to infer the pH of the top and bottom samples. The pH inferences were validated using analog matching, and an examination of inferences from triplicate cores in four lakes. In general, pH

changes were small in comparison to other acid-sensitive regions. The relatively short pH gradient, comparatively higher pre-industrial pH values, and the amount of acid deposition are factors that may explain these trends. The use of a single, multi-indicator reconstruction model for inferring pH is discussed, with special reference to lake management.

Finally, a regional increase in the taste and odour-causing chrysophyte, *Synura petersenii*, was observed in lakes in south-central Ontario. This increase was unrelated to observed changes in lakewater pH, and indicates that the threat of taste and odour events has greatly increased in these lakes since pre-industrial time. Possible explanations for this trend are discussed.

CO-AUTHORSHIP

This thesis has been written in publication format, and all of the manuscripts are co-authored by my supervisors, Dr. B. Cumming and Dr. J. Smol, who provided me both with intellectual advice and financial assistance. Chapter 2 is also co-authored with Dr. J. Blais (U. of Ottawa) and Dr. R. France (Harvard), who were involved in the development of the project, and collected the sediment cores. Dr. Blais provided the ^{210}Pb chronologies. I performed all of the laboratory and statistical work associated with the scaled chrysophyte analysis, and authored the manuscript. Dr. S. Dixit (Queen's) is a co-author on Chapter 3, which involved the development and assessment of three inference models for reconstructing lakewater pH. This chapter incorporates lakes that were analysed for chrysophytes by Dr. Dixit and others, the results of which have been published elsewhere. Dr. Dixit also provided valuable comments on drafts of the manuscript. I enumerated the chrysophytes from the Ontario lakes, completed all of the statistical analysis, and prepared the manuscript found in Chapter 3. Chapters 4 and 5 include Dr. Roland Hall (U. of Waterloo) as a co-author, as he was involved in the development stages of the work in south-central Ontario. The chrysophyte laboratory work, statistical analysis, and the preparation of the manuscripts were performed by me for both of these chapters.

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CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

General introduction and outline of thesis chapters

The province of Ontario contains more than 250,000 freshwater lakes, representing approximately one quarter of Canada's freshwater supply. The majority of these lakes are situated in boreal or mixed-boreal regions, and are underlain by igneous bedrock of the Canadian Shield. Historically, these softwater, nutrient-poor lakes have been relatively isolated from human disturbances. However, in recent decades, lakes within the boreal shield have been subjected to a growing number of anthropogenic stressors that threaten their ecological integrity, and today they are among the most threatened freshwater ecosystems in the world (Schindler, 1998).

Natural and anthropogenic disturbances occur both at a watershed-scale, such as clearcut logging (Keenan and Kimmins, 1993) and forest fires (Schindler et al., 1980), and at a regional-scale, including the deposition of strong acids from long-range sources and climatic change (Dillon et al., 1987; Schindler et al., 1996; Schindler, 1997; Stoddard et al., 1999). Disentangling the relative effects of these factors on water quality is complicated because they act synergistically in many lakes, and climate may play a confounding role (e.g. Schindler et al., 1996; Yan et al., 1996). Despite growing evidence that water quality may be adversely affected by these disturbances, few studies have attempted to quantify these effects relative to background or 'natural' conditions in Canadian Shield lakes.

The impact of anthropogenic stressors on water quality of Canadian Shield lakes is poorly understood due to a scarcity of long-term data. While more than twenty years of monitoring data exist in some regions of the boreal shield (e.g. Experimental Lakes Area, Muskoka-Haliburton), even these are too short in duration to evaluate changes relative to natural or pre-disturbance conditions (e.g. pre-industrial). In the absence of these data, the science of paleolimnology may be used to reconstruct past environments from information archived in lakes sediments (Smol, 1992).

The main objective of this thesis is to assess the impacts of multiple stressors on the water quality of Canadian Shield lakes in northwestern and south-central Ontario, Canada. I examine the effects of major watershed disturbances (e.g. logging and forest fires), and the deposition of strong acids, on long-term changes in water quality. Scaled chrysophytes preserved in lake sediments are used as indicators of environmental change.

The term "water quality", which is used throughout the thesis, refers to the physical and chemical conditions that define the lake environment, as they are important both to human populations, who rely on these ecosystems for drinking and recreational purposes, and to the biological assemblages that exist within these ecosystems. Ultimately, changes in water quality may alter the structure and function of biological communities. Furthermore, due to the increasing number and magnitude of these stressors, there is evidence that these changes may be unprecedented in many lakes.

This thesis is composed of four manuscripts that have been prepared for publication. The first manuscript (Chapter 2) assessed the effects of major watershed disturbances (e.g. forest harvesting, forest fires) on the water quality of lakes in

northwestern Ontario, Canada. Using a "Before-After-Control-Impact" experimental design (Underwood, 1991), I evaluated the response of scaled chrysophyte taxa to the removal of greater than 90% of the watershed vegetation in the disturbance lakes. This manuscript has been published in the *Canadian Journal of Forest Research* (Paterson et al., 1998). The version that appears here has been updated, but the changes do not alter the overall interpretation of our original findings.

Chapters 3, 4 and 5 follow a logical sequence of work conducted in south-central Ontario. This region differs from northwestern Ontario in that it receives higher levels of acidic deposition (Jeffries et al., 1995), and other human influences are generally greater. Chapters 3 and 4 involve the development and application of statistical models for inferring lakewater pH in Ontario shield lakes. In the first chapter, I develop and assess the performance of intra-, inter-regional, and Modern Analog Model (MAT) reconstruction models for inferring pH from scaled chrysophyte assemblages. In Chapter 4, I use one of the models to reconstruct the pH of modern (present-day) and fossil (pre-industrial) sediment samples from approximately 50 lakes in south-central Ontario. I discuss the impact of acidic deposition on regional changes in water quality. I also introduce a single, multi-indicator reconstruction model, developed from scaled chrysophyte (Chapter 3), chrysophyte cyst (Wilkinson et al., 1999), and diatom (Hall and Smol, 1996) inference models, which may be of particular interest to lake managers.

Finally, in Chapter 5, I discuss the importance of changes in the chrysophyte species assemblage in south-central Ontario lakes that are unrelated to long-term changes in lakewater pH. These findings indicate that there has been a regional increase in the

taste and odour causing chrysophyte, *Synura petersenii*, indicating that the threat of such episodes are much greater now than in pre-industrial times. I discuss possible hypotheses that may explain these trends. A general discussion and conclusions are found in Chapter 6. Relative abundance species data have been included in a series of Appendices.

Literature review

Each of the manuscripts prepared for this thesis provide reviews of relevant literature in their respective introductions. Therefore, I review only the most important themes in the section that follows.

Paleolimnology and environmental change

Paleolimnology is the science that uses the physical, chemical and biological information archived in lake sediments to reconstruct and interpret past environmental conditions (Smol and Glew, 1992). Over the past two decades, paleolimnology has developed from a predominantly qualitative science to a quantitative tool that has been used to assess important issues related to long-term environmental change (Smol, 1992). Recent advances in field sampling (Glew, 1988, 1989), laboratory techniques (Cumming et al., 1990), and statistical analysis (Birks, 1995, 1998) have dramatically increased the power and reliability of paleolimnological studies.

A knowledge of pre-disturbance conditions and natural variability are essential requirements of effective ecosystem management (Smol, 1992). While direct historical records are the preferred sources of such data, they are often absent, too short in duration,

or of questionable quality to be used by lake managers. There are a number of advantages of using paleolimnogical techniques to obtain long-term data. First, the sediment record provides an archive of past environmental change which may be used to evaluate changes in water quality relative to natural variability (e.g. changes in climate). Second, long-term records are evaluated using consistent methodology, a detail that is often absent in contemporary studies of environmental change. Finally, in studies in which the variability of biological assemblages is compared before and after known disturbances (e.g. Chapter 2), paleolimnology allows for a balanced statistical design over long time periods (e.g. decades).

Quantitative tools in paleolimnology

The use of ordination statistics and regression and calibration techniques in paleolimnology have been discussed elsewhere in detail (Birks, 1995, 1998). Briefly, ordination techniques may be used to detect patterns in modern species data (i.e. surface sediment samples) and environmental variables collected from a suite of lakes, to identify lakes which are outliers with respect to species assemblages or their environment, and to determine which of the measured environmental variables can be inferred downcore (ter Braak, 1986; Birks et al., 1990a; Birks, 1995, 1998). Regression and calibration techniques may then be used to model species' responses to individual environmental variables (regression), and to use the resulting inference model to infer past environmental conditions from the fossil species assemblage (calibration) (Birks, 1995).

The environmental reconstructions that are obtained may be validated in a number

of ways, although direct comparison with measured variables downcore is the most reliable method (Fritz, 1990). However, historical data do not exist in many systems, and indirect validation techniques may be applied. Birks et al. (1990a) have suggested three numerical approaches that may be used in this respect. For example, the root mean square error of prediction (RMSEP) of individual fossil samples may serve as a relative measure of the reliability of the reconstructions. In addition, fossil samples can be plotted passively onto ordination axes that are constrained by the modern species and environmental data. Goodness-of-fit statistics, such as the squared residual distance to the ordination axis, may be used to assess the reliability of the reconstructions (e.g. Laird et al., 1996). Analog matching also may be used to identify fossil assemblages with poor analogs in the modern training set. A distribution of lowest minimum dissimilarities may be calculated for all samples in the modern data set. Fossil samples with dissimilarities greater than the 95% percentile of this distribution, when compared with the modern samples, are considered to have poor analogs (e.g. Chapter 3).

The Modern Analog Technique (MAT) is a conceptually simple reconstruction approach that provides an alternative to regression and calibration techniques (Birks, 1995). Based simply on measures of dissimilarity, MAT does not rely on an underlying statistical model (e.g. linear or unimodal species-environment response) (Birks, 1995). The environmental conditions of each fossil sample are calculated as (weighted) means of measured variables from one or more modern samples, selected based on their similarity to the fossil species assemblage. In contrast to regression-based reconstruction techniques, the Modern Analogue Technique (MAT) has rarely been used in

paleolimnology. However, in recent comparisons with regression-based reconstruction models, MAT has performed as well as unimodal-based regression techniques (Lotter et al., 1999; Olander et al., 1999).

Analysis of Similarities (ANOSIM) is a non-parametric, re-sampling procedure that can be used to test the null hypothesis of no difference in species assemblages following known perturbations (e.g. Chapter 2) (Clarke and Warwick, 1994). ANOSIM is preferable to the multivariate analysis of variance (MANOVA), as it does not assume approximate (multivariate) normality of the species data, which is likely to be violated in relative abundance data with many zero values (Clarke and Warwick, 1994). Based on a rank similarity matrix, ANOSIM tests the null hypothesis in three steps. A test statistic (R-stat), which contrasts the rank similarities of samples between time periods (i.e. before and after the disturbance) with the rank similarities within time periods (i.e. before or after the disturbance), is calculated. Next, using a re-sampling procedure with replacement, a null distribution of the R-statistic is generated. In the final step, the original test statistic is compared to the null distribution to calculate a significance level.

Scaled chrysophytes: General ecology and their use in paleolimnology

Chrysophycean algae (chrysophytes), members of the classes Synurophyceae and Chrysophyceae (Andersen, 1987), are a diverse group of predominantly freshwater organisms. Chrysophytes often dominate the phytoplankton of north-temperate, oligotrophic lakes (e.g. Sandgren, 1988; Eloranta, 1995), but are widely distributed and exist in other environments, including tropical, polar and alpine regions (Wallen and

Allen, 1982; Rott, 1988; Cronberg, 1989). Taxa are typically planktonic, although benthic and epiphytic species exist (Sandgren, 1988).

Chrysophytes are generally well distributed along many environmental gradients, including lakewater pH, conductivity, temperature, and trophic status (Roijackers and Kessels, 1986; Sandgren 1988; Siver, 1991a; Duff, 1994; Siver 1995). While many chrysophyte taxa have well defined ecological optima and tolerances along these gradients, pH is commonly cited as the most important variable influencing scaled chrysophyte distributions (Cumming et al., 1992a; Dixit et al., 1992; Dixit et al., 1999).

The scaled chrysophytes, representing approximately 20% of known chrysophycean taxa (Duff et al., 1995), produce siliceous scales, bristles, and spines that form part of the sedimentary record, and can be used to differentiate between taxa (Smol, 1995). The number of scales produced by different species may vary, and therefore scale abundances provide an indirect measure of true cell abundances. While correction tables to convert scales to cell numbers exist (Siver, 1991b), Cumming and Smol (1993) have shown these corrections make little difference to the performance of quantitative reconstruction models.

The earliest applications of scaled chrysophytes as indicators of environmental change involved long-term examinations of changes in lake trophic status (e.g. Munch, 1980; Smol, 1980; Smol et al., 1983). The first studies were qualitative in approach, and as of yet, few studies have attempted to apply quantitative inference models to reconstruct past trophic status (Siver et al., 1999). However, there is evidence that scaled chrysophytes are responsive to changes in nutrient status, as is evident from experimental

studies of artificial fertilization (Dixit et al., 1990; Zeeb et al., 1994).

Lakewater pH is considered to be the most important variable influencing the distribution of scaled chrysophytes. For this reason, these organisms are considered to be excellent indicators of lake acidification, and numerous quantitative inference models have been developed for inferring pH in many regions, including Ontario (Dixit et al., 1992), Adirondack Park (Cumming et al,. 1992a), northeastern USA (Siver and Hamer, 1990; Dixit et al., 1999), and Europe (Birks et al., 1990b; Cronberg, 1990). In Adirondack Park, these models were used to infer pH changes since pre-industrial times, providing convincing evidence that the timing and spatial extent of lake acidification was compatible with the deposition of strong acids from industrial sources (e.g. Cumming et al., 1992b, Cumming et al., 1994). In other regions, these models have been validated against measured environmental data (Dixit et al., 1989).

Recently, scaled chrysophytes have been used to infer changes in water quality associated with watershed disturbances (Rhodes and Davis, 1995), land-use (Marsicano and Siver, 1993; Lott et al., 1994), and taste and odour events (Nicholls and Gerath, 1985; Nicholls, 1995). Clearly, these organisms are sensitive indicators of environmental change, and are of particular use in Canadian Shield lakes, where they constitute an important part of the phytoplankton biomass.

Ecological differences between scaled chrysophytes and diatoms may explain why there are often differences between inferences made using these two algal indicators. For example, scaled chrysophytes are planktonic organisms, while diatoms have representatives from planktonic, benthic and epiphytic habitats. Variability in the

chemical conditions of different regions of the lake may explain some variance in the inferences between diatoms and chrysophytes (Siver et al., 1999). Second, spatial variability with respect to vertical position within the water column may also contribute to the variability between these two organismal groups. Large, colonial chrysophyte taxa may form population maxima below the thermocline (Sandgren, 1988). These highly mobile, flagellated colonies may experience an advantage of being in a zone of reduced competition, while gaining access to nutrients in the hypolimnion (Sandgren, 1988). Third, there exist seasonal differences with respect to the timing of maximum abundance in north-temperate lake ecosystems, which may also reflect differences in the chemical conditions of lakes. For example, in lakes receiving acidic deposition, an acid pulse associated with snowmelt is likely to affect chrysophyte populations more than diatoms, as chrysophytes often dominate the phytoplankton at this time in early spring, immediately after ice-out (Smol et al., 1998).

The impacts of watershed disturbances on lake ecosystems

There is growing evidence that watershed disturbances, including logging and forest fires, may significantly alter water quality and quantity in stream ecosystems (Bormann et al., 1974; Nicholson et al., 1975; Feller and Kimmins, 1984; Miller et al., 1997). However, studies examining the effects of watershed disturbances on lake ecosystems are rare, and few have examined these disturbances relative to pre-disturbance conditions. For example, in a recent review of the 'Impacts of Forest Harvesting on Lake Ecosystems' (Miller et al., 1997), less than 5% of studies assessed changes in water

quality relative to a minimum of two years of pre-disturbance data, and the duration of many of the studies was less than five years. Therefore, there is a need for long-term studies that evaluate the impacts of watershed disturbances on water quality, relative to natural variability.

It is difficult to make broad generalizations with respect to the effects of logging and forest fires on lake ecosystems because findings have been contradictory in many studies. Also, the impacts from logging and forest fires may differ, depending on the intensity of the disturbances, and the physical and chemical conditions that existed in the lake at the time of the disturbance (Enache and Prairie, 2000). Several recent studies from boreal lakes in Québec (Carignan et al., 2000; Lamontagne et al., 2000), and Alberta (McEachern et al., 2000), suggest that watershed disturbances may significantly alter water quality. Although these impacts are often short-lived, they may impact biological assemblages in some lakes (Enache and Prairie, 2000; Patoine et al., 2000; Planas et al., 2000). However, studies in northwestern Ontario (Paterson et al., In Press; Steedman, 2000; Steedman and Kushneriuk, 2000), and British Columbia (Laird and Cumming, In Press; Laird et al., In Press) have shown minimal changes in lakes following watershed disturbances. These authors also conclude that climatic factors were potentially more important in some of these systems. Similarly, in a regional survey of the effects of logging and forest fires on the water quality of Ontario shield lakes, climate was determined to have a greater influence on changes in water quality than major watershed disturbances (Blais et al., 1998; Paterson et al., 1998).

There are several explanations that may explain the discrepancies across studies.

Differences in water residence time, largely regulated by morphometric factors (e.g. lake volume, drainage ratio), may be an important determinant of the degree of impact that is detected. Small lakes with large, steeply sloping watersheds (e.g. Mud Pond, Maine: Rhodes and Davis, 1995), and short water residence times, may be more sensitive to disturbances in their catchments. Furthermore, the relative influence of regional factors, such as acidic deposition and climatic conditions (e.g. drought), may have played an important role in some regions (e.g. Schindler et al., 1996). For example, northwestern Ontario experienced a significant warm and dry period during the time period of the paleolimnological studies (e.g. Blais et al., 1998; Paterson et al., 1998).

The acidification and recovery of Ontario shield lakes

The processes controlling the acidification and recovery of lakes in Ontario shield lakes are complex. A decline in the deposition of sulphate in the Sudbury and Muskoka-Haliburton regions since the early 1980s has produced variable results (Dillon and LaZerte, 1992; Stoddard et al., 1999; Keller et al., 1992). In south-central Ontario, there is little evidence of recovery following a 30-40% decline in sulphate loads (Stoddard et al., 1999). In part, these trends may be the result of a depletion of base-forming cations from watershed soils from decades of acidic deposition (Likens et al., 1996). The re-oxidation and release of reduced sulphur stored in wetlands has also been recognized as a contributing factor delaying the recovery of acidified lakes (Yan et al., 1996), which may be linked to abnormally dry periods, such as years following El Niño events (Dillon et al., 1997a). In contrast, many lakes in the Sudbury region have shown a marked

improvement in water quality following reduced acid loads (Dixit et al., 1989; Keller et al., 1992, Smol et al., 1998). In part, this may reflect differences in the degree of impacts experienced across regions. Historically, deposition has been much greater in the Sudbury region (Lazerte and Dillon, 1984; Keller et al., 1992), and therefore the relative decrease in acid deposition may have been greater in the Sudbury region. Other factors, such as pre-industrial pH values (Cumming et al., 1994; Smol et al., 1998), and hydrological factors such as water renewal time, may also be important. For example, within-lake alkalinity generation is greater in lakes with longer renewal times (Schindler, 1986).

Recent paleolimnological studies of the effects of acid deposition on lakes in south-central Ontario (Hall and Smol, 1996; Wilkinson et al., 1999), and in other regions (Cumming et al., 1992b), suggest that alkaline lakes (pH > 7) have increased in pH since pre-industrial times. Several mechanisms, including watershed disturbances (Rhodes and Davis, 1995), cation exchange, and sulphate and nitrate reduction in watershed soils wetlands, and lake sediments may have contributed to these observed increases in alkalinity (e.g. Dillon et al., 1997b; Schindler, 1986). These processes will be further regulated by watershed characteristics, such as the underlying geology and the presence of wetlands, and by interaction of these factors with climate (Yan et al., 1996).

While contemporary studies of the impact of anthropogenic disturbances on water quality provide useful information, they are often too short in duration to estimate change relative to background or pre-disturbance conditions in aquatic ecosystems. This problem

may be overcome through the use of paleolimnology, which uses the information recorded in lake sediments to reconstruct past environments, and to determine the timing of change (Smol, 1992). Scaled chrysophytes are sensitive environmental indicators that have been used often in paleoecological studies in north-temperate regions. These organisms are ecologically diverse, well preserved in lake sediments, and respond rapidly to environmental change (Smol, 1995). In this thesis, I apply paleolimnological techniques to assess the impact of watershed and regional disturbances, namely logging, forest fires, and acid deposition, on water quality in Canadian Shield lakes. By providing a long-term perspective, I evaluate impacts relative to pre-disturbance conditions in these lakes. This work was conducted on Canadian Shield lakes in northwestern and south-central Ontario, Canada.

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CHAPTER 2

ASSESSMENT OF THE EFFECTS OF LOGGING, FOREST FIRES AND DROUGHT ON LAKES IN NORTHWESTERN ONTARIO: A 30-YEAR PALEOLIMNOLOGICAL PERSPECTIVE

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Abstract: The frequency and intensity of large-scale watershed disturbances (e.g. logging and forest fires) are increasing in northwestern Ontario. Timber-harvesting and wildfires have been shown to alter water quantity and quality in stream ecosystems. Unfortunately, scientific studies of these impacts on lakes are rare. Using paleolimnological techniques, we examined the remains of scaled-chrysophytes in sediment cores from four lakes that have had the majority of their watersheds clear-cut, two lakes that have had large forest fires in their watersheds, and two lakes that have had minimal watershed disturbance. Lakes in this study showed minor changes in the composition of scaled chrysophytes at a temporal resolution of two to four years, despite removal of more than 90% of the forest. Furthermore, temporal variability in the species assemblages were similar in all lakes. A gradual change in the species assemblages of all lakes suggested a regional influence may have been responsible. We hypothesize that hydrological changes brought about by a regional drought from 1970-1990 may have exerted an overriding influence on lakes over this time period.

Introduction

In northwestern Ontario, forests are becoming increasingly disturbed by forest fires and timber-harvesting (Wotton and Flannigan 1993; Overpeck et al. 1990; Schindler 1998). For example, several General Circulation Models predict that the frequency and intensity of forest fires will increase in the boreal forest with climate warming (Schlesinger and Mitchell 1987; and see review in Moser 1996). A twenty-year (1970-90) warming and drying period reported in northwestern Ontario may be evidence that climate change has already begun (Schindler 1998; Schindler et al. 1996). Additional regional changes in the boreal forest are occurring due to human activities. Timber-harvesting has been shown to alter water quantity and quality in stream ecosystems (Feller and Kimmins 1984; and see review in Keenan and Kimmins 1993, and Miller et al. 1997). For example, in small watersheds at the Experimental Lakes Area (ELA) in northwestern Ontario, Nicolson (1975) detected short-lived changes in water chemistry, stream temperature and pH, with a return to pre-disturbance conditions two to three years following clear-cutting. Unfortunately, scientific studies of the effects of forestry on lake ecosystems are rare (Keenan and Kimmins 1993).

Lakes are functionally linked to geological, meteorological, and biological processes that occur within their catchments, and within airsheds (Likens and Bormann 1974, 1979). Alterations to lake watersheds, occurring naturally or anthropogenically, may trigger limnological changes in lakes. Wildfires, windthrow, and timber-harvesting have been shown to increase catchment erosion, thereby altering mineral and nutrient input into aquatic systems (Likens and Bormann 1974; Schindler et al. 1980; Bayley et al.

1992*a*, 1992*b*; Beaty 1994; Rhodes and Davis 1995). Increased inputs of dissolved organic carbon (DOC), and dry fallout of particulates from large, regional wildfires have also been linked to watershed disturbances (Schindler et al. 1992). These impacts, among others, influence the physical, chemical, and biological characteristics of the aquatic environment. The underlying geology, watershed morphology, vegetation, soil depth, and biological trophic interactions are all factors that potentially influence the response of a lake to a disturbance. Over a longer time-frame, climate may play an influential role in regulating changes in lakes through changes in precipitation and evaporation ratios, hydrology, and vegetation (see reviews in Schindler 1997, 1998).

The biological, chemical, and physical histories of lakes and their watersheds may be partially reconstructed from the sediment record (Smol 1992; Dixit et al. 1992*b*). Through paleolimnological analyses, this information can be extracted to infer past aquatic and terrestrial conditions, and to determine the timing and degree of change in lake ecosystems. This information is not attainable from contemporary studies of watershed disturbances. Additionally, the paleolimnological approach allows for an examination of many years of a lake's history over a relatively short time period. This cost-effective technique can therefore be used to help evaluate ecological and environmental change.

Scaled chrysophytes, taxonomically members of the algal classes Synurophyceae and Chrysophyceae, have been used extensively in paleoecological studies (see review in Smol 1995). The siliceous body scales of these organisms preserve well in lake sediments, often occurring in large abundances. Body scales of chrysophytes are

generally identifiable to the species level, allowing for reconstruction of past chrysophyte populations. Furthermore, scaled chrysophyte taxa have well-defined ecological optima and tolerances, and can be used quantitatively to monitor past environmental change (Smol 1988).

Scaled chrysophytes are effective indicators of lake eutrophication (Smol 1980; Smol et al. 1983; Zeeb et al. 1994), lake acidification (Smol et al. 1984; Dixit et al. 1992*a*; Cumming et al. 1992, 1994), land-use (Marsicano and Siver 1993; Lott et al. 1994), and climate change (Siver and Hamer 1992; Cumming et al. 1993). It has been suggested that scaled chrysophytes may be more sensitive to environmental change than other paleoindicators (e.g. diatoms). For example, in some paleolimnological studies of lake acidification and recovery, the ecological response of scaled chrysophytes has been shown to pre-date diatom changes (Dixit et al. 1990*b*, 1992*a*).

The remains of scaled chrysophytes preserved in lake sediments have been used to infer changes in pH, conductivity, and trophic status associated with fire and windstorm events (Rhodes and Davis 1995), anthropogenic forest removal (Lott et al. 1994), and cultural development in lake watersheds (Smol 1995). The ecological sensitivity of scaled chrysophytes to changes in their environment, coupled with their relatively straightforward taxonomy, make these organisms ideal paleoindicators for studying the effects of watershed disturbances on lakes.

The purpose of this study was to determine, using paleolimnological techniques, whether lakes in northwestern Ontario (Table 1) have responded to known large-scale watershed disturbances. Here, we examined the remains of scaled-chrysophytes in ^{210}Pb-

dated sediment cores from four lakes that have had their watersheds clear-cut, two lakes that have had large forest fires in their watersheds, and two lakes that have had minimal disturbance in their watersheds (i.e. reference lakes). Temporal changes in the relative abundance of species-specific chrysophyte scales preserved in lakes sediments were used to determine the influence of large-scale watershed disturbances in comparison to natural variability over the last 25-35 years.

Study area and study lakes

All our study lakes are located in NW Ontario between Thunder Bay and Kenora, Ontario (Figure 1). This region is characterized by southern boreal forest, with an overlap into Great Lakes/St. Lawrence forests. Dominant tree species include jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). All the lakes lie on Precambrian bedrock, overlain by glacial morainal deposits and shallow, discontinuous sandy soils (Brunskill and Schindler 1971; CLEW 1994).

Eight distinct lake basins were selected for coring (Table 1). Four lake basins (442, m4w, m6n, and m6s) were categorized as "cut" lakes. The watershed of ELA lake 442 was clear-cut during the winter months of 1975-76 (19 ha), 1977-78 (21 ha), and 1978-79 (53 ha), leaving only a narrow buffer strip (McCullough and Campbell 1993). Lakes m4w, m6n and m6s are located approximately 200 km southwest of ELA (lake basins m6n and m6s are two distinct basins of the same lake). The watersheds of these lake basins were clear-cut to shoreline in the spring of 1983 by the Great Lake Paper

Company (France et al. 1996; France 1997*a,b*). Following the removal of commercial timber, re-growth of native tree species was facilitated by the burning of the logging slash. During the harvest period, a logging road was constructed within the watershed of lake m6n (Blais et al. 1998). In the catchments of all "cut" lakes the re-growth of forests has been rapid and unhindered.

Two lakes, bn1 (Percy) and bn2 (Little Joe), were categorized as "burn" lakes. Situated just NW of the ELA along the Trans-Canada highway, the watersheds of these lakes were burned to shoreline by a severe forest fire in 1980 (France 1997*a*). At ELA, the 1980 fire was extremely severe, resulting in the destruction of 20-50 cm organic mats in some watersheds (Schindler 1998). As a result, re-vegetation in watersheds burned by this fire has been slower, and sparser than in the watersheds of "cut" lakes.

Lakes 26-1 and 42-2 were categorized as "reference" lakes. Situated approximately 250 km southeast of the Experimental Lakes Area (ELA) (Brunskill and Schindler 1971), the watersheds of these lakes have been subjected to little (0-5%) disturbance over the last ~ 70 years (France and Peters 1995). The catchments of lakes 26-1 and 42-2 form part of the Coldwater Lakes Experimental Watersheds project, and are currently being studied by the Ontario Ministry of Natural Resources (CLEW 1994).

Materials and Methods

Field: Using a Glew (1989) gravity corer equipped with a modified trigger mechanism and a core tube (approximately 50 cm in length, internal diameter 6.35 cm), duplicate sediment cores were collected by Blais et al. (1998) from the eight ice-covered lake

basins in March, 1995. Lake sediment cores were extruded vertically on site using a Glew close-interval extruder (Glew 1988) into the following sub-samples: 0.5-cm intervals for the top 5-cm; 1-cm intervals between 5 and 10 cm; 2-cm intervals between 10 and 20 cm; and 5-cm intervals for the rest of the core. Sediment was transferred immediately to plastic Whirlpak® bags and transported to the laboratory for cold storage (at approx. 4°C). In September 1996, six of the eight lake basins were re-visited to collect additional physical-chemical data (Table 1). Lake basins m6n and m6s were not visited, as heavy undergrowth in their catchments prevented accessibility to the shores of these lakes.

Lab: By measuring the ^{210}Pb activity of every sediment interval (see Blais et al. 1995 for details), a temporal chronology was established for each lake. Species-specific fossilized remains of scaled chrysophytes were isolated from sediment samples using a standard acid digestion technique (see Wilson et al. 1996 for details). The resulting aliquot from each sample was diluted with distilled water and pipetted onto individual coverslips, and allowed to evaporate. Samples were mounted onto glass slides using Naphrax®, a mounting medium with a high-refractive index (R.I. = 1.7). Under a Leica DMRB light microscope with phase-contrast optics, a minimum of 400 chrysophyte scales were enumerated at 1600X (100X objective, 16X ocular lens) from transects, ensuring adequate coverage of at least half of the coverslip. From each core, the top 15 sediment sub-samples (i.e. the top 10 cm, representing approximately the last 25-35 years) were examined for chrysophyte scales. Taxonomic identification of scales was based on: Siver

(1991, 1993), Takahashi (1978), Wee (1982), Kling and Kristiansen (1983), Nicholls (1982, 1988), and through discussion with colleagues. Scales from a few species were grouped into the categories of *Mallomonas* 'small' and *Mallomonas* 'medium', due to difficulty in identifying these scales to the species level with the light microscope. In any lake, these categories accounted for no more than 10% and 5% respectively of the total relative abundance of all species.

Statistical analysis: A total of 25 taxa were identified from all the lakes examined. Of these, eight species were considered rare (did not achieve > 1% relative abundance in a minimum of four lakes), and were eliminated from statistical analyses. The remaining species data were log (x+1) transformed, where x was the original species abundance, to reduce the impact of very abundant species (e.g. *Mallomonas duerrschmidtiae* Siver, Hamer & Kling). The sediment intervals within each lake were reduced in number from 15 to 10 by combining 0.5-cm samples into 1-cm samples. This was done to produce approximately even-aged sediment intervals, at an inter-sample resolution of between two to four years. To standardize the time period examined across lakes, all samples pre-dating 1960 were eliminated. This resulted in two fewer samples for lakes 42, bn1 and m6s.

Non-metric multi-dimensional scaling (nMDS) was used to ordinate the species data, using the statistical package Primer v.4.0 (Plymouth Marine Laboratory 1994). Ordinations produced by nMDS use the rank dissimilarities (Euclidean distance dissimilarity matrix) to adjust the position of samples in multidimensional space, until the

ranked inter-point distances best approximate the original ranked dissimilarities (Clarke and Warwick 1994). The resultant two-dimensional ordination represents between-sample dissimilarities through time. Thus, the distance between any two points represents the relative dissimilarity of the species assemblages of two sediment intervals.

Increased species variability over a given time period can be used as a relative measure of disturbance, in which samples from disturbed study sites often yield greater temporal variability than those from control sites (Warwick and Clarke 1993). To qualitatively assess if the variability in species composition was greater in "cut/burn" lakes relative to "reference" lakes, an Index of Multivariate Dispersion (IMD) was calculated within each lake as a relative measure of variability in the species composition through time (Clarke and Warwick 1994). This was achieved by contrasting the average rank dissimilarities from the original Euclidean distance dissimilarity matrices of "reference" and "cut/burn" lakes from the early 1960s to 1995. IMD values were averaged and standardized to a value of "1". Values greater and less than "1" represented above and below average variability in species composition, relative to other lakes.

Sediment intervals were categorized *a priori* into pre- and post-catchment disturbances for lakes with impacted watersheds and pre- and post-1983 for the "reference" lakes. "Reference" lakes were included in these calculations to allow for a standardized comparison of species change across all lakes (1983 was selected as a cut-off point as it represented the year of disturbance in three "cut" lakes). Within each grouping, sediment intervals were treated as replicates. The null hypothesis of no difference in chrysophyte species composition between groups in each lake was tested

using an Analysis of Similarities (ANOSIM), a non-parametric test analogous to a multivariate one-factor ANOVA (Clarke and Green 1988; Clarke and Warwick 1994). Between sample pairs, within- and across-group rank dissimilarities were computed, shuffled, re-calculated repeatedly (10,000 times), and compared to the original rank dissimilarities to calculate a significance (p) value. ANOSIM produced a R-statistic for each analysis (between "1" and "-1"), indicative of the strength of the statistical relationship. R = 1 when all replicates within groups were more similar to one another than any replicates from other groups, and vice versa for a R value of "-1" (Clarke and Warwick 1994).

The probability of making a Type I statistical error, in which the null hypothesis is rejected when H^{o} is true, increases with the number of comparisons made. To account for this a Bonferroni correction may be used, in which the significance level for individual comparisons is adjusted based on the number of tests performed (see Pagano and Gauvreau, 2000 for details). However, in studies in which statistical power is likely to be low (e.g. low sample sizes), reducing the significance level with a Bonferroni test may increase the likelihood of making a Type II statistical error. As a result, the null hypothesis may be incorrectly accepted (Pagano and Gauvreau, 2000). In environmental impact studies, a Type II error may be more of a concern than a Type I error, as it decreases the ability to detect significant impacts where they exist. For this reason, Bonferroni corrections were not performed in this study.

Results

The chrysophyte species assemblages observed in this study are typical of oligotrophic, Canadian Shield lakes in Ontario (Kling and Kristiansen 1983; Nicholls 1982, 1988; Nicholls and Gerrath 1985, Zeeb et al. 1994) (Figure 2a,b). In five of the eight lakes examined, *Mallomonas duerrschmidtiae* Siver, Hamer & Kling attained relative abundances of over 30%. This species, only recently separated taxonomically from *M. crassisquama* (Asmund) Fott, is commonly found in slightly acidic, oligotrophic lakes of low conductivity (Siver 1991, 1995; Cumming et al. 1992). Other common taxa were *Synura spinosa* Korshikov and *S. petersenii* Korshikov, the latter of which is considered to be an ecological generalist. In two lakes (m4w and bn1), *S. sphagnicola* (Korshikov) Korshikov occurred in relative abundances of over 30%. At the time of sampling, these lakes had a dark, tea colour, and had relatively shallow Secchi depths of 1.8 and 2.3 m, respectively. This may reflect a distinct preference of *S. sphagnicola* for coloured, humic waters (Siver 1987; Dixit et al. 1990*a*). Relative to differences between lakes, temporal changes in the chrysophyte species assemblages were subtle in individual lakes (Figures 2a,b, 3). The most similar species assemblages occur in the "cut" lakes m6n and m6s, two distinct lake basins of the same lake (Figure 3).

Greater species variability associated with watershed disturbances was not apparent in this study. "Reference" lakes, on average, were of equal or greater variability through time than "cut/burn" lakes (Table 2). In particular, "reference" lake 26-1 was the most variable, and the "burn" lakes the least variable over the time period examined (Table 2).

In each lake, sediment intervals were divided *a priori* into two groups: before and after watershed disturbances (or before and after 1983 in "reference" lakes). The null hypothesis of no difference in the similarities between chrysophyte species assemblages was tested in each lake, and could not be accepted in five of the eight lakes examined (Table 3). In general, the "reference" lakes showed the greatest difference in species assemblages before and after 1983, as indicated by higher R values (Table 3). "Cut/burn" lakes bn1, m6s, and m6n showed significant, but weaker differences in species assemblages before and after catchment disturbances. Lakes 442, m4w, and bn2 did not show a significant difference in species assemblage across groups.

Discussion

Contemporary studies of the impacts of logging and forest fires on watersheds have shown that the removal of catchment vegetation can alter the physical, chemical, and biological components of lake ecosystems. Disturbance of the landscape can result in increased watershed erosion, disrupting mineral and nutrient balances in aquatic systems, and increasing suspended sediments in lakes (Likens and Bormann 1974; Schindler et al. 1980; Bayley et al. 1992*a*, 1992*b*; Beaty 1994; Rhodes and Davis 1995). Dissolved organic carbon (DOC), the most abundant dissolved input from the catchment in oligotrophic lakes (Schindler et al. 1997), may also increase in lakes following watershed clear-cutting, or decrease in lakes in which the watershed has been severely burned (Schindler et al. 1992). Furthermore, major forest disturbances have been shown to affect lake water pH, through a disruption in the relative inputs of base cations and acid anions

from catchment soils (Nicolson 1975; Rhodes and Davis 1995; Korhola et al. 1996; Schindler et al. 1996).

Limnological changes resulting from watershed disturbances were not apparent in our lakes, as determined through an examination of chrysophyte populations in lake sediment cores. Our results suggest that clear-cutting and wildfire have had little effect on these study lakes, despite removal of over 90% of the forest in the disturbance lakes. The composition of chrysophyte populations in our study lakes remained relatively stable through time, at a temporal resolution of two to four years. Changes in the relative abundances of chrysophyte taxa, considered to be sensitive indicators of environmental change were subtle, and gradual (Figures 2a,b). Furthermore, the temporal variability of chrysophyte populations was not greater in disturbance lakes then in "reference" lakes (Table 2). These findings are supported by an on-going study of the effects of timber-harvesting on lakes at the Coldwater Lakes Experimental Watershed (CLEW 1994) in northwestern Ontario. In the first year following major watershed clear-cuts (30-70% of catchment), nutrient levels have shown no consistent pattern in reference (n = 2) and cut (n = 3) watersheds, relative to five years of pre-disturbance data (Steedman et al., In Press). Furthermore, analysis of chlorophyll *a* levels, summer thermocline progression, and the relative abundance of phytoplankton species have revealed no significant differences one year following clear-cutting at CLEW (Steedman et al., In Press).

The magnitude of limnological change following watershed deforestation may be regulated by site-specific characteristics. For example, the presence of a buffer strip in the watershed of one lake (442) and rapid regrowth of vegetation in a watershed may

minimize the loss of nutrients from the catchment (Marks and Bormann 1972), and shorten the period of increased runoff often associated with clear-cutting (Patric 1980). In our study, regrowth of vegetation proceeded rapidly, with re-colonization of the watershed by native tree species (e.g. *Pinus banksiana* and *Picea mariana*). As a result, impacts in our study lakes may have been short-lived, and undetectable at a temporal resolution of two to four years. Furthermore, morphometric characteristics such as the ratio of watershed to lake area, lake volume, and the slope of the catchment may also influence how lakes respond to watershed disturbances. In general, small, shallow lakes with large, steeply-sloped watersheds are the most susceptible to limnological changes following deforestation (Keenan and Kimmins 1993; Rhodes and Davis 1995; Miller et al. 1997). The watershed areas of our study lakes were relatively small in size (less than 100 ha in 6 lakes -- Table 1), with shallow slopes (max. relief = 60 m -- Steedman personal communication), and may have been less sensitive to disturbances within their catchments.

Watershed-level characteristics may provide a partial explanation for the minimal species changes observed in the disturbance lakes. However, the subtle temporal changes in chrysophyte populations observed in both "reference" and "burn/cut" lakes suggest that a regional factor may have influenced the limnology of these lakes over the last 25-35 years. Below, we discuss the importance of climate (e.g. a regional drought) as a potential factor regulating water quality in the study lakes.

Evidence of regional change: Drought as a possible controlling mechanism?

Limnological changes directly attributable to watershed disturbances were not evident in our study lakes. Temporal changes in the relative abundance of chrysophyte taxa were subtle in both "reference" and "cut/burn" lakes relative to other studies that have used scaled chrysophytes as indicators of environmental change (Figure 2a, 2b) (Cumming et al. 1994; and see review in Smol 1995). Furthermore, the temporal variability of species assemblages was similar in all lakes (Table 2), and significant differences were found in chrysophyte populations before and after watershed disturbances (and before and after 1983) in "reference" and "cut/burn" lakes (Table 3). These findings suggest that limnological changes may be the result of regional-scale processes over the past 25-35 years. Unusually warm and dry weather characteristic of drought conditions were recorded in northwestern Ontario from 1970-1990 (see Schindler 1997, 1998 for detailed review of impacts on lakes). Due to an increase in average annual air temperature and a decrease in precipitation, there was an approximate 70% decrease in surface runoff from catchments reported at ELA over this time period. Reduced runoff coupled with increased rates of evaporation were responsible for a severalfold increase in water renewal times in many lakes at ELA. While elevated water renewal time increased the concentrations of many inorganic chemicals, a decrease in total phosphorus, silica and dissolved organic carbon (DOC) was found, presumably a result of reduced annual exports from the catchment, and alterations in biogeochemical processes within the lake (Schindler et al. 1996, 1997; Curtis and Schindler 1997). The removal of DOC caused an increase in lake transparency, resulting in larger zones of photosynthetic activity, a

deepening of the thermocline, and weaker stratification (Schindler et al. 1996).

In a recent study, Blais et al. (1998) linked marked changes in sedimentation patterns in our study lakes to the 1970 to 1990 drought. An examination of ^{210}Pb-cumulative dry mass curves revealed significant declines in slope near the surface in six of the eight sediment cores examined in our study. These inflections, apparent in sediment cores from "reference" and "cut/burn" lakes, provide evidence of a regional decrease in sedimentation rate occurring after 1981 ± 1.9 years (Blais et al. 1998). Observed sedimentation rates declined by an average of 80%, a value proportional to the approximate 70% decrease in surface runoff recorded at ELA over the same time interval. Furthermore, these findings differed from previous studies that have reported increases in sedimentation rates following watershed deforestation (Flower et al. 1987; Dearing 1991). This pattern was not apparent in "reference" lake 42-2 or "burn" lake bn2, the latter of which showed potential evidence of mixing near the surface of the core (Blais et al. 1998). In general, lake 42-2 is hydrologically different from the other lakes as it has a relatively small watershed area (Table 1), and does not have a channelized inflow (Steedman et al. In Press). Therefore, changes in sedimentation rate resulting from decreased stream inputs and reduced erosion from the catchment may not have been important in lake 42-2 (Blais et al. 1998).

Chrysophyte species assemblages differed significantly before and after the early 1980s in five of eight study lakes (Table 3). Although species changes were subtle and gradual (Figures 2a,b), some commonalities exist. In six lakes, there were increases in the relative abundances of *Chrysosphaerella* spp. Lauterborn em. Nicholls and/or *Synura*

petersenii Korshikov, concurrent with a decrease in the relative abundance of *Mallomonas duerrschmidtiae* and/or *S. spinosa* Korshikov. In New England, similar shifts have been linked to the anthropogenic alteration of watersheds, including logging (Lott et al. 1994), urbanization, and agriculture (Marsicano and Siver 1993). Lott et al. (1994) suggest that logging in the catchment of a small Pennsylvanian lake may have increased inputs of dissolved ions and sediment matter, leading to an increase in lake water conductivity. In our study, these patterns were apparent in both "reference" and "cut/burn" lakes, with species changes commencing before the disturbances (Figure 2a,b). Therefore, it is unlikely that these findings are a result of logging or forest fires. A possible hypothesis is that the 1970-1990 drought may have been responsible for a small, regional increase in conductivity. Similar to findings at ELA (Schindler 1997, Schindler et al. 1996), an increase in water renewal times may have caused elevated concentrations of inorganic ions in lakes. However, gradual species changes were not observed in diatom populations (Paterson et al. In Press), which have been shown to be sensitive indicators of conductivity changes (Stoermer and Smol 1999).

A gradual change in water transparency is a second hypothesis that may explain the observed trends in chrysophyte assemblages, that were not found in the diatom assemblages. During the 1970-1990 drought at the ELA, Schindler et al. (1990, 1996) noted a significant increase in water transparency, primarily due to a decrease in DOC concentrations in lakes (i.e. decreased export from watershed, and increased in-lake removal). These changes resulted in a deepening of the thermocline, and an increase in the zone of sub-thermocline production (Schindler et al. 1990, 1996). Colonial (e.g.

Synura), and large unicellular chrysophytes (e.g. *Mallomonas caudata*), which increased in our study lakes, may selectively form deep-water peaks below the thermocline (Sandgren, 1988). Large chrysophytes are often successful in clear lakes when the photic zone extends beyond the thermocline, a pattern that was detected at the Experimental Lakes Area during a twenty-year drought (Schindler et al., 1990). Furthermore, deep-water populations, dominated by large, flagellated chrysophytes, may also have an advantage over epilimnetic taxa, as they may be protected from increased UV-B radiation associated with increased water transparency (Leavitt, et al., 1999; Xenopoulos et al., 2000).

The significant decreases in sedimentation rates (Blais et al. 1998), in combination with the subtle, regional changes in chrysophyte species assemblages suggest that a twenty-year drought may have had a significant influence on the limnology in many of our study lakes. Most importantly, the effects of increased watershed erosion often associated with deforestation (e.g. increases in the influx of nutrients, DOC, suspended sediment) may have been reduced by large decreases in surface runoff (up to 70% at ELA) in the watersheds of these lakes. Thus, climate may have exerted an overriding influence on these lakes (through changes in hydrology), with changes in the watershed exerting a secondary role. In closing, these results support the long-term climate change research conducted in northwestern Ontario. At ELA, the limnological impacts of watershed disturbances (forest fires and windthrow) were outweighed by the gradual limnological changes that occurred in study lakes as a result of reduced water flow during the 1970 to 1990 drought (see Schindler 1997, 1998; Schindler et al. 1996 for

details).

Summary

Lakes in this study showed minor changes in the species composition of scaled chrysophytes at a temporal resolution of two to four years, despite removal of over 90% of the catchment vegetation or complete burns of the watershed. A gradual change in the chrysophyte species assemblages of both "reference" and "cut/burn" lakes suggested that a regional influence may have been responsible for our findings. We propose that climate may exert a dominant influence on these lakes, with changes in a lake's watershed exerting a secondary role. Future attempts at disentangling the relative importance of these two factors would benefit from examining multiple indicators of environmental change at a variety of temporal scales, as impact detection is dependent on the ecological response of taxa, as well as the temporal scale of the study. Finally, an increase in sample size (e.g. the number of lakes examined) may provide a greater regional signal, recognizing that there is a trade-off between the number of lakes that can be analysed and temporal resolution at which each lake is studied.

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Table 1. Summary of physical-chemical variables of the study lakes.

	Lake 26 (ref)	Lake 42 (ref)	bn1 (burn)	bn2 (burn)	Lake 442 (cut)	m4w (cut)	m6n (cut)	m6s (cut)
Longitude:	92°08'	92°10'	94°06'	94°51'	94°49'	92°12'	92°11'	92°11'
Latitude:	49°07'	49°05'	49°46'	49°51'	49°46'	49°15'	49°15'	49°15'
Lake area (ha):	30	26	39	10	6	22	14	19
Watershed area (ha):	88	44	170	87	145	42	76	21
Watershed/ Lake area:	2.9	1.7	4.4	8.7	9.1	1.9	5.9	1.1
z-max (m):	37	17	30	--	18	12	13	13
Coring depth (m):	36	17	19	12	15	9	13	13
% basin disturbed:	5 (1987)	0	100 (1980)	100 (1980)	65 (1975-79)	90 (1983)	99 (1983)	99 (1983)
Specific cond. (µS):	21.7	14.8	142.7	160.2	25.3	17.6	--*	--
pH:	6.7	6.7	6.6	6.4	6.7	6.5	--	--
Secchi (m):	7.9	6.3	2.3	3.3	4.1	1.8	--	--

* "--" no data are available

Table 2. Summary of temporal variability within lakes, with respect to chrysophyte species assemblages.

Lake	Index of Multivariate Dispersion (IMD)*
Cut lakes	
Lake 442	1.19
m4w	1.01
m6n	1.07
m6s	0.92
Burn lakes	
bn1	0.88
bn2	0.58
Reference lakes	
Lake 26	1.23
Lake 42	1.06

* IMD of 1 represents average value

Table 3. Summary of ANOSIM results, before and after catchment disturbances (and before and after 1983 in reference lakes).

Lake	Pre-dist. time period	Post-dist. time period	R-stat	p-value
Cut lakes				
442	1966-1980	1980-1995	-0.02	0.51
m4w	1961-1983	1983-1995	0.17	0.10
m6n	1976-1983	1983-1995	0.36	0.04
m6s	1962-1983	1983-1995	0.62	0.04
Burn lakes				
bn1	1963-1980	1980-1994	0.67	0.02
bn2	1972-1980	1980-1995	0.15	0.22
Reference lakes				
26-1	1967-1983	1983-1995	0.69	0.02
42-3	1960-1983	1983-1995	0.79	0.02

Figure captions

Figure 1. Map showing the three study areas in northwestern Ontario, Canada. Cross-hatched boxes represent regions containing study lakes.

Figure 2a. Stratigraphies of the relative abundance of species through time in "burn" and "reference" lakes. Estimated ^{210}Pb dates are shown alongside the core depth. Dotted lines represent disturbance horizons (or the year 1983 in "reference" lakes).

Figure 2b. Stratigraphies of the relative abundance of species through time in "cut" lakes. Estimated ^{210}Pb dates are shown alongside the core depth. Dotted lines represent disturbance horizons.

Figure 3. Ordination of nMDS values. Each transect represents a different lake through time. Inter-point distances reflect the relative dissimilarity of species assemblages between sediment intervals. All lakes were included in the nMDS calculation.

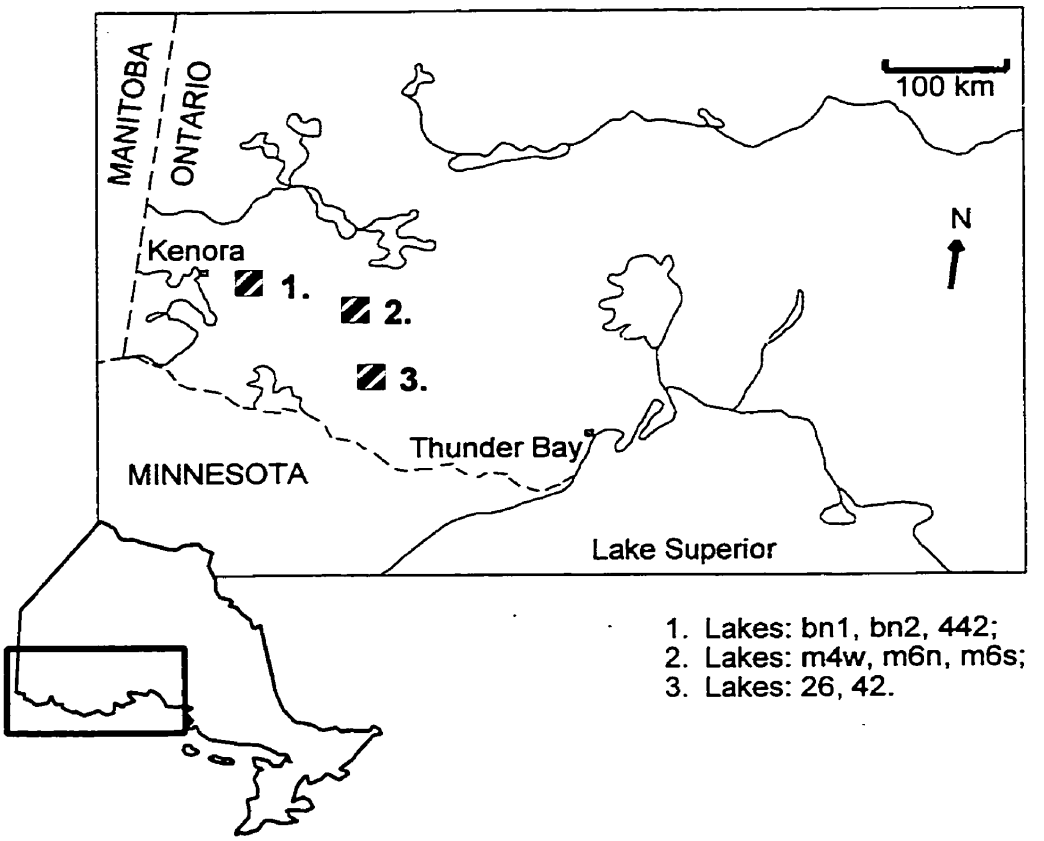
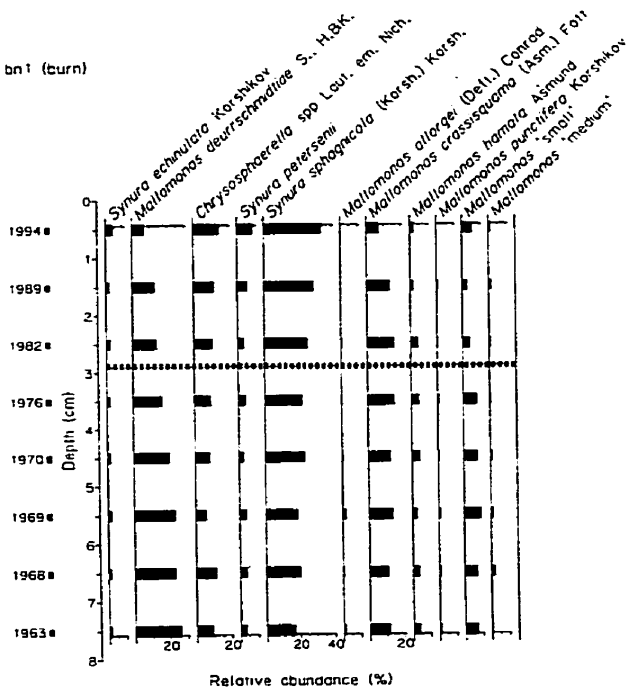
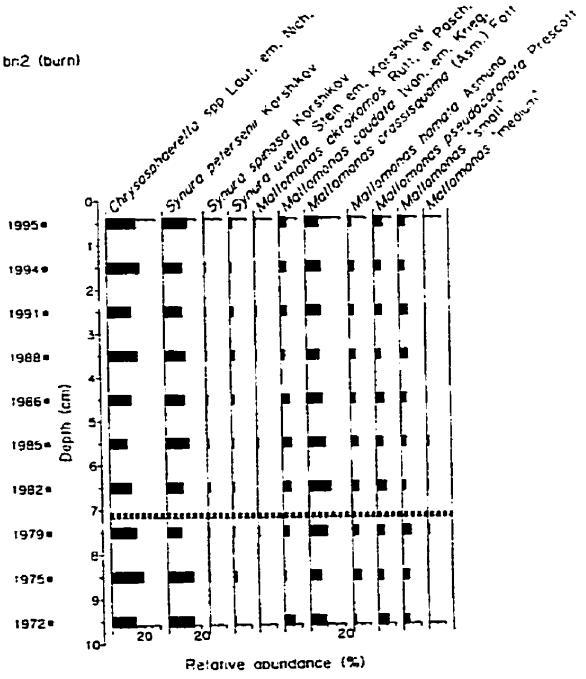

MANITOBA
ONTARIO
100 km
N
Kenora
1.
2.
3.
Thunder Bay
MINNESOTA
Lake Superior
1. Lakes: bn1, bn2, 442;
2. Lakes: m4w, m6n, m6s;
3. Lakes: 26, 42.

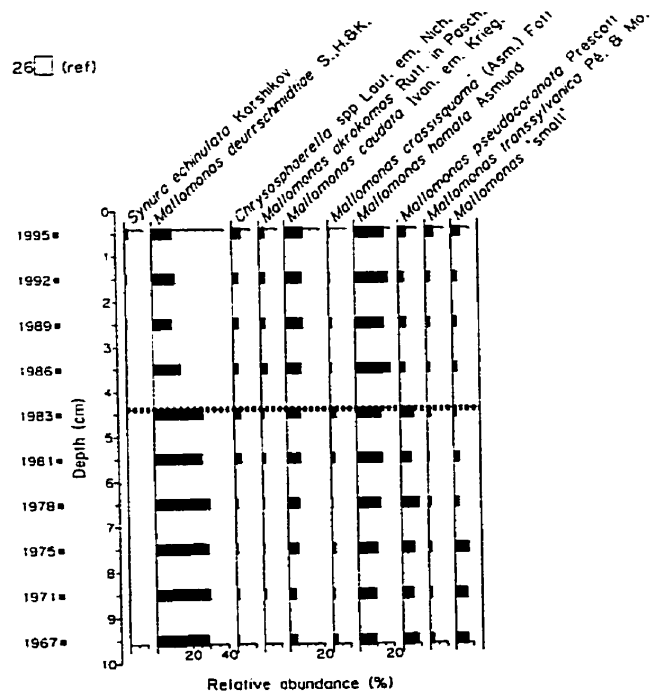
Figure 1

Burn lakes:





Reference lakes:



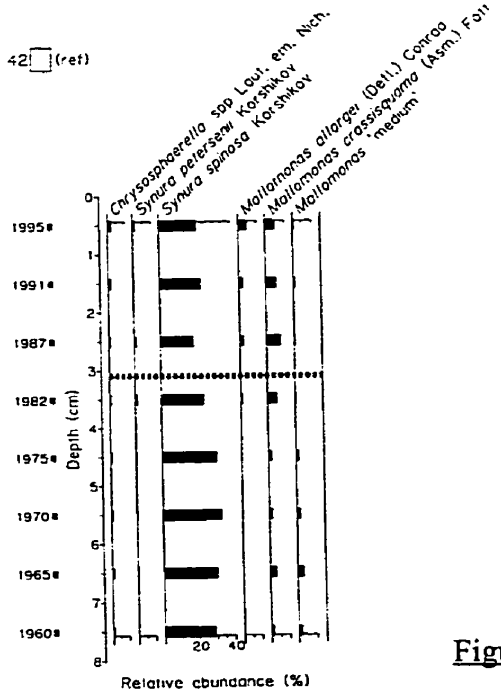


Figure 2a

Cut lakes:

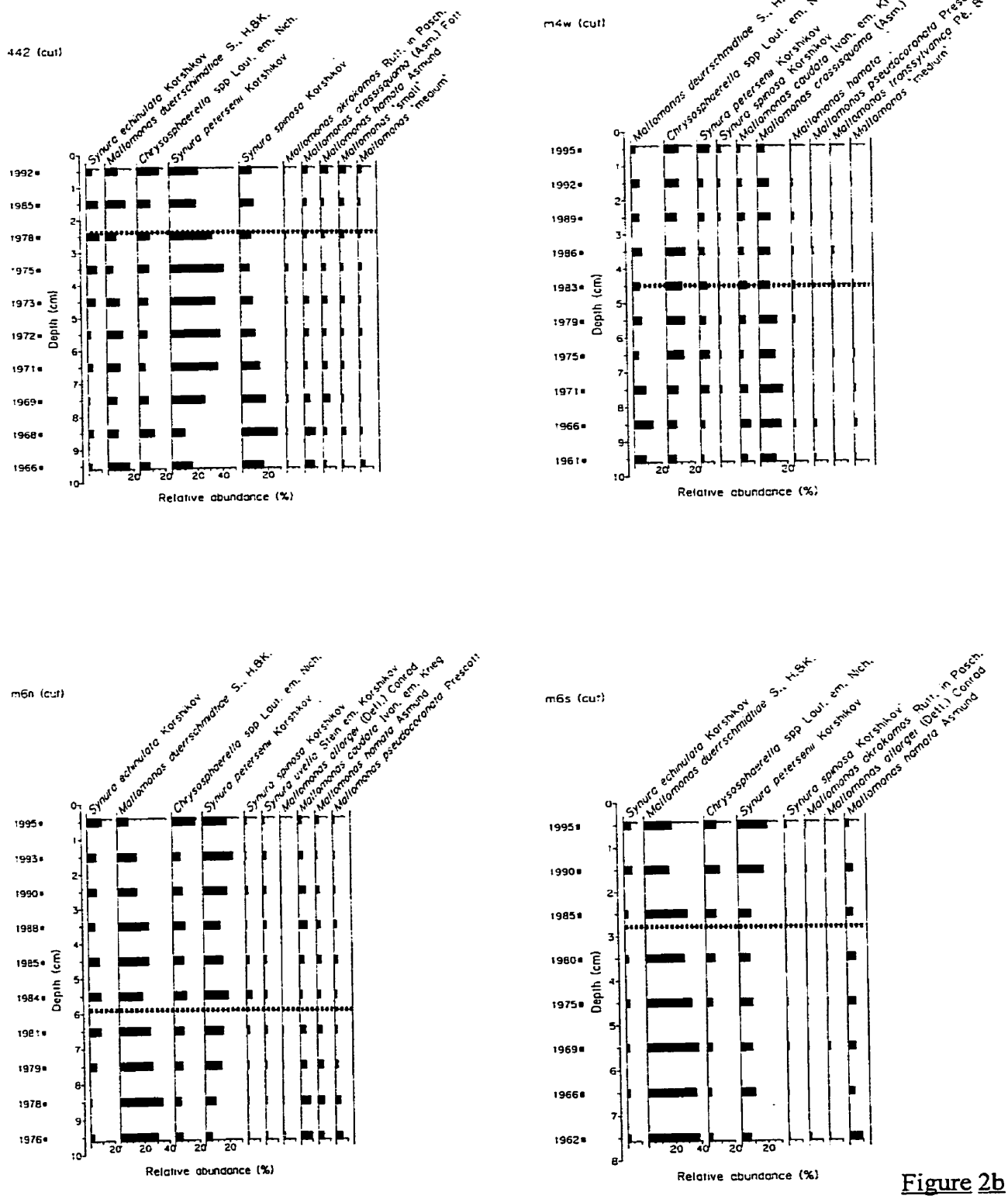


Figure 2b

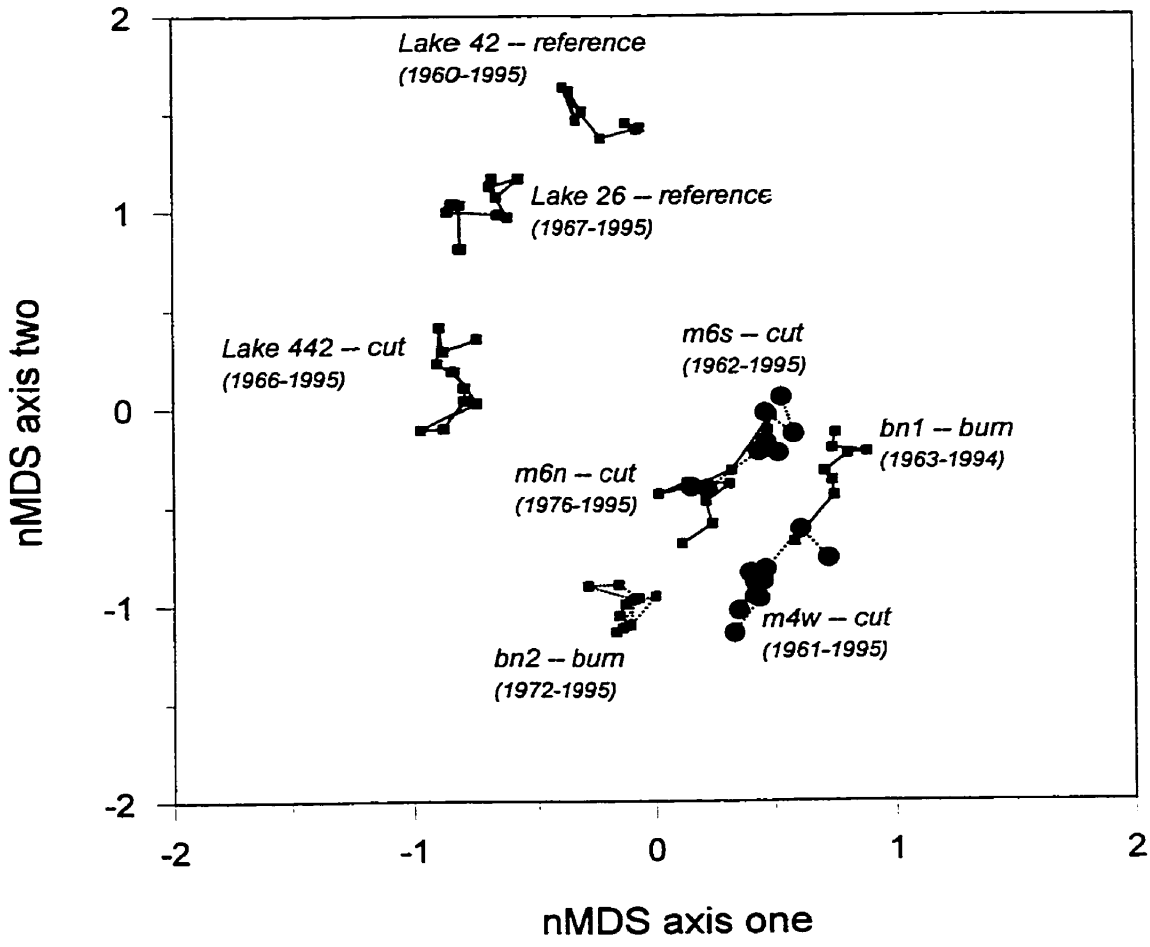

Lake 42 -- reference
(1960-1995)
Lake 26 -- reference
(1967-1995)
Lake 442 -- cut
(1966-1995)
m6s -- cut
(1962-1995)
bn1 -- burn
(1963-1994)
m6n -- cut
(1976-1995)
m4w -- cut
(1961-1995)
bn2 -- burn
(1972-1995)
nMDS axis two
nMDS axis one
2
1
0
-1
-2
-2
-1
0
1
2

Figure 3

CHAPTER 3

THE IMPORTANCE OF MODEL CHOICE ON PRESENT-DAY AND PRE-INDUSTRIAL pH INFERENCES FROM SCALED CHRYSOPHYTE ASSEMBLAGES IN ONTARIO SHIELD LAKES

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Key words: Inference models, Modern Analog Technique, chrysophytes, lakewater pH, Ontario shield lakes

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Abstract

The selection of a reliable inference model is the most crucial step in developing ecologically-sound reconstructions of environmental variables in the past. We compared intra-, inter-regional, and Modern Analog Technique (MAT) reconstruction models in their ability to infer lakewater pH from scaled chrysophyte assemblages. The performance of each model was assessed by examining cross-validated coefficients of determination and prediction errors, and through reconstructing the pH of 48 modern and fossil samples in south-central Ontario, Canada. Using the intra- and inter-regional data sets, we found little difference in the ability of the regression-based models to infer pH. Partial Least Squares (PLS) regression, Weighted Averaging (WA), and Weighted Averaging Partial Least Squares (WA-PLS) inference models for pH showed similar values for jack-knifed coefficients of determination (r^2_{jack}), root mean squared errors of prediction ($RMSEP_{jack}$), and mean biases. Based on an analog matching approach, the inferred values from 48 top-bottom sediment samples in south-central Ontario lakes suggested that the intra-regional model did not provide reliable reconstructions for approximately half of the fossil samples. However, inferences from the Modern Analogue Technique (MAT), and the inter-regional reconstruction models, were found to have appropriate analogs and thus considered to be more reliable. We conclude that the inter-regional WA-PLS model provided good estimates of pH, as it did not suffer from the poor analog problem, and was less variable than the MAT model.

Introduction

The primary aim of many paleolimnological studies is to reconstruct past environments from the biological assemblages preserved in lake sediments. For this purpose transfer functions may be developed from a number of modern surface-samples and corresponding environmental variables. First, a regression step is used to model the relationship between the contemporary species assemblage and an environmental variable of interest (e.g., pH). A second step, termed calibration, applies the modeled responses to infer past environments from fossil species assemblages. For reconstructions to be valid, the training set of modern samples and environmental variables must represent the range of species assemblages and environmental conditions that have occurred in the past, and samples (modern and fossil) must be of consistent taxonomy and quality (Birks, 1998). The selection of an appropriate training set is an important first step in the development of ecologically-sound reconstruction models.

The size of the data set is often limited by the relatively short duration of most studies. Intra-regional training sets, usually consisting of fewer than 100 lakes, are commonly used in paleolimnology. These smaller, region-specific training sets are thought to be more homogenous than larger data sets. For example, large data sets may suffer from taxonomical or methodological errors which result from the involvement of more than one analyst (Birks, 1994). Furthermore, there may exist biogeographical differences in the distribution of taxa (Lotter et al., 1999), or ecotypic variation which translate to differences in the ecological optima and tolerances of taxa along environmental gradients. In contrast, inter-regional or combined training sets may extend

the environmental gradient of interest, thereby allowing more accurate estimates of the ecological parameters (e.g., optima, tolerances) of species. Moreover, a large modern training set increases the likelihood of finding good analogs for fossil samples, a necessary component of reliable reconstructions (Birks, 1998).

Few studies have critically evaluated the performance of intra- versus inter-regional statistical models in the reconstruction of environmental variables. Lotter et al. (1999) determined that a combined, inter-continental inference model for reconstructing paleotemperature from fossil midges provided similar reconstructions to those of the intra-regional models. While the inferred rate and magnitude of change differed among models, comparable patterns of change were detected. Walker et al. (1997) found that an expanded chironomid inference model for inferring paleotemperature greatly improved climate reconstructions from a pond in Atlantic Canada, suggesting that the original model underestimated the magnitude of late glacial temperature change. An expanded reconstruction model (217 lakes) for inferring lakewater pH from scaled chrysophyte assemblages was created by combining a training set of 71 lakes in Adirondack Park (Cumming et al., 1992a), and 146 lakes in northeastern USA (Dixit et al., 1999), although the performance of the model relative to its component parts has not been undertaken (Dixit et al., 1999).

In contrast to regression-based reconstruction techniques, the Modern Analogue Technique (MAT) has rarely been used in paleolimnology (see Lotter et al., 1999; Olander et al., 1999). MAT is considered to be an intuitively and conceptually simple means of reconstructing one or more environmental variables, and is not based on an

underlying statistical model of species response along an environmental gradient (e.g., linear or unimodal species-environment response) (Birks, 1995). Based simply on measures of similarity, MAT reconstructs the past environment of fossil samples as a mean (or weighted mean) from a pre-determined number of modern samples. Modern samples with species assemblages most similar to the fossil sample are selected for the reconstruction. In recent comparisons with regression-based reconstruction models from chironomids, MAT has performed as well as unimodal-based regression techniques, including weighted averaging regression and calibration (Lotter et al., 1999; Olander et al., 1999). MAT has not yet been applied to scaled chrysophyte assemblages to reconstruct environmental variables.

Lakewater pH is one of the most important environmental variables influencing the distribution of scaled chrysophytes (Siver, 1995; Smol, 1995). Numerous studies have demonstrated that regression-based reconstruction models with scaled chrysophytes as environmental indicators can reliably infer the pH of fossil samples (e.g. Cumming et al., 1992b; Dixit et al., 1992). In some cases, this has been verified by matching inferred values with direct measurements over periods of rapid environmental changes in pH (Dixit et al., 1989a). The strong relationship between pH and chrysophyte assemblages, make chrysophytes ideal environmental indicators for comparing the relative performance of reconstruction models.

This study critically examines the impact of model choice on present-day and pre-industrial pH inferences from 48 shield lakes in south-central Ontario. We develop two regression-based models, and a MAT model, that can be used to infer the pH of lakes in

Ontario. The first regression model is derived from a training set of 53 lakes in south-central Ontario (Hall & Smol, 1996). The larger, inter-regional regression model, and the MAT model, are created using a 117-lake training set from south-central Ontario (Hall & Smol, 1996), Adirondack Park (Cumming et al., 1992a), and northeastern USA (Dixit et al., 1999), respectively. First, the models are used to predict the pH of 53 modern samples from lakes in south-central Ontario. Second, we infer the pH of 48 fossil samples, and use indirect validation techniques to assess the reliability of the reconstructions made from each of the three models.

Methods

Sample collection and preparation details from the south-central Ontario and northeastern USA lakes are presented in Hall & Smol (1996) and Dixit et al. (1999), respectively. All of the sediment cores were collected from the deepest basin of each lake, and the top 0.5 to 1-cm of each core was sectioned on-site using a Glew vertical extruder (Glew, 1988). The fossil samples from the south-central Ontario lakes were collected as 1-cm increments from a depth of 20-cm or greater, and are representative of the pre-industrial time period (Hall & Smol, 1996). Scaled chrysophytes were enumerated by two research scientists at the Paleoecological Environmental Assessment and Research Laboratory, and taxonomy was harmonized through discussions and the preparation of a photographic archive. Prior to statistical analysis, ambiguous taxa were grouped into broader categories (e.g. *Mallomonas* 'small') to ensure that taxonomy remained consistent across regions. The inference models only included taxa that were present in at least two lakes,

at a relative abundance of at least 1% in one of the lakes.

Measured pH values were plotted against detrended correspondence analysis (DCA) axis one scores from the 53-lake and 117-lake data sets. The strength of the relationship was used to evaluate whether pH tracked an important direction of variation in the training sets. Detrended canonical correspondence analysis (DCCA), with pH as the sole constraining variable, was performed to determine whether linear or unimodal modeling techniques were most appropriate when developing regression-based inference models. The statistical program CANOCO version 4 (ter Braak & Šmilauer, 1998) was used for these analyses.

The intra- and inter-regional data sets were examined independently using square-root transformed species data to reduce the influence of very dominant taxa (e.g. *Synura petersenii*), and to produce superior inference models (cf., Cumming & Smol, 1993). Principal components analysis (PCA) of the environmental data, and DCA of the species data were used to screen for samples outliers. Samples falling above the 95% confidence interval of both the PCA and DCA axis one sample scores were considered to be outliers. No samples were found to be outliers in either the intra- or inter-regional training sets. The statistical package CALIBRATE version 0.54 (Beta) (Juggins & ter Braak, unpublished program) was used to compare the results from Partial Least Squares (PLS), Weighted Averaging (WA) (with and without tolerance down-weighting) with inverse and classical deshrinking, and Weighted Averaging Partial Least Squares (WA-PLS) regression models. The jack-knifed coefficient of determination (r^2_{jack}), root mean square error of prediction ($RMSEP_{jack}$), and the mean biases were used as relative measures of

the performance of each model (Birks, 1998).

The statistical program ANALOG version 1.6 (Line & Birks, unpublished program) was used to develop the MAT model. MAT-inferred pH values were calculated for each of the modern samples and plotted against measured pH values. The jack-knifed r^2 and the RMSEP were estimated from the mean and a weighted mean (weighted by the dissimilarity) of the 1,2,...,10 closest matches. All tests were performed on square-root and untransformed species data, using both the Bray-Curtis and Euclidean dissimilarity measures. The simplest model that gave the highest r^2_{jack} and lowest $RMSEP_{jack}$ was selected for the reconstructions.

The regression-based inference models that performed best from each of the intra- and inter-regional training sets, and the MAT model were used to estimate the pH of modern samples of 53 lakes in south-central Ontario. For each model, measured values were plotted against predicted values, and the jack-knifed coefficient of determination and residual structures were compared.

The pH of fossil samples was inferred from 48 lakes in south-central Ontario (Hall & Smol, 1996) using the best intra- and inter-regional inference models, and the MAT model. The following criteria were used to evaluate the ability of the models to reconstruct the pH of fossil samples (Birks, 1998). First, bootstrapped standard errors of prediction for all modern and fossil samples were estimated using the statistical program WACALIB version 3.3 (Line et al., 1994). Prediction errors from fossil samples were compared to a distribution of errors from the modern samples. Fossil samples with errors greater than the 95% percentile of the error distribution from the modern samples were

considered to be poor reconstructions. Second, analog matching was used to identify fossil assemblages with poor analogs in the modern training set. Using the statistical program ANALOG, a distribution of lowest Bray-Curtis dissimilarities was calculated for all samples in the modern data set. Fossil samples with dissimilarities greater than the 95% percentile of this distribution, when compared with the modern samples, were considered to have poor analogs.

Results and Discussion

Developing models for inferring pH

Regression-based models

The pH gradient of the 53-lake data set was narrower than that of the 117-lake set (Table 1). The latter, which included lakes from the smaller training set, was created to provide an even distribution of samples along the pH gradient (Figure 1). Samples within each pH range were randomly selected from the 270-lake training set from south-central Ontario (53 lakes: Hall & Smol, 1996), Adirondack Park (71 lakes: Cumming et al., 1992a), and additional lakes from the northeastern USA (146 lakes: Dixit et al., 1999).

In the 117-lake training set, 34 taxa were identified in a minimum of two lakes, at a relative abundance of at least one percent in one lake (Table 2). Three taxa present in the inter-regional training set were not found in the south-central Ontario lakes. An additional six taxa included in the inter-regional training set were deleted from the 53-lake training set as they were extremely rare. In general, the taxa that were missing or

eliminated from the intra-regional inference models had pH optima towards the ends of the measured pH gradient.

Scatter plots of observed pH versus detrended correspondence analysis (DCA) axis one scores showed strong linear correlations for the 53-lake and 117-lake training sets, indicating that pH tracked an important direction of variation in the species data (Figure 2). A detrended canonical correspondence analysis (DCCA) with pH as the sole constraining variable revealed a compositional gradient of less than 2 SD units for the 53-lake model, suggesting that linear methods would be most appropriate for developing inference models (Birks, 1995). For the 117-lake model, a compositional gradient of greater than 2 SD units indicated that unimodal methods would be more appropriate (Table 1), although we tested the use of both linear and unimodal reconstruction models.

Partial least squares (PLS) and weighted-averaging partial least squares (WA-PLS) (2 components) regression models provided higher jack-knifed coefficients of determination and lower errors of prediction than the WA models developed using the 53-lake training set (Table 3). Due to the short gradient length of DCCA axis 1 constrained to pH, and a lower mean bias, PLS was considered to be the best model for inferring pH with the data set. WA-PLS (2 components) proved to be the best model using the 117-lake training set, resulting in the strongest overall measures of the coefficient of determination, prediction error, and mean bias (Table 3). The ability for WA-PLS to outperform WA has been noted in other studies (e.g. ter Braak & Juggins, 1993), and may result from two main factors. First, WA-PLS tends to have a greater reduction in the edge effect commonly associated with WA, in which the response curves

of taxa near the ends of the pH gradient are truncated, resulting in poor estimates of their pH optima (Birks et al., 1990; ter Braak & Juggins, 1993). Second, WA does not consider the influence of additional environmental variables on the biological assemblage, which often provide additional structure to the data (Birks, 1995). In contrast, WA-PLS uses the additional structure left in the residuals to improve the estimation of taxa optima (Birks, 1998).

On average, inter-regional models produced a jack-knifed RMSEP twice as large as the intra-regional models (Table 3). This was likely the result of differences in the length of the pH gradients (Table 1), as error estimates are constrained by the environmental gradients used in their development (Walker et al., 1997). To make comparisons across training sets the errors were standardized as a percentage of the gradient lengths. Standardized errors for the 53-lake and 117-lake training sets were found to be similar, equaling 12% and 11% of gradient lengths, respectively. The cross-validated error estimates from the 117-lake models are comparable with published results from North American inferences models, with values ranging from 0.41-0.69 pH units (Cumming et al., 1992a; Dixit et al., 1999; Siver et al., 1999).

Modern Analog Technique (MAT)

As with WA models (Cumming & Smol, 1993), the MAT reconstruction model improved when the species data were square-root transformed. The choice of the dissimilarity coefficient (i.e., Bray-Curtis versus Euclidean) made little difference in the performance of the model. The Bray and Curtis (Bray & Curtis, 1957) dissimilarity was selected for

developing the model, and for reconstructions, as it is intuitively simple, and gives equal importance to all taxa (Prentice, 1980). The use of a weighted mean in the estimation of inferred values did not improve the model, and therefore a standard mean was used for the analysis. As the number of closest matches was increased from one to four, there was an increase in the jack-knifed r^2 and a decrease in the jack-knifed RMSEP of the model (Figure 3). Increasing the number of closest matches from four to ten resulted in only a minor improvement in the jack-knifed r^2 and error values, suggesting that four closest matches produced the simplest model for inferring pH (Figure 3).

In developing the MAT model, the pH of modern samples was estimated using a training set of the four closest matches, excluding the modern sample for which pH was being inferred (Birks, 1995). In this manner, a jack-knifed r^2 and error estimate was calculated from observed and predicted values, allowing for a direct comparison with the regression-based inference models. Applying the 117-lake training set, MAT produced a higher coefficient of determination and lower error of prediction than regression-based models. However, the mean bias was also highest for the MAT model (Table 3), which showed the largest discrepancies between measured and predicted values at the ends of the pH gradient. A closer examination revealed that MAT underestimated and overestimated the measured pH of alkaline and acidic lakes, respectively. This represents a potential drawback of MAT reconstructions, which may be less reliable towards the ends of the gradient (Birks, 1995), in cases where there is poor a poor representation of samples at the gradient extremes. A similar pattern, termed the edge effect, may also be encountered using WA regression. In this case, the response curves of taxa with optima

near the ends of the environmental gradient may be truncated resulting in poor estimates of taxa optima and of measured pH (Birks et al., 1990).

Using the pollen record from Elk Lake to reconstruct climate, Bartlein and Whitlock (1993) determined that regression, MAT, and response-surface approaches produced similar reconstructions. Furthermore, MAT models have performed as well as regression-based techniques when used to infer lakewater and air temperatures from fossil chironomid assemblages (Lotter et al., 1999; Olander et al., 1999). Despite these encouraging results, MAT has not yet been used extensively in paleolimnological reconstructions. Although it is the least statistical of the reconstruction approaches (Bartlein & Whitlock, 1993), it requires a large, comprehensive training set which covers a range of biotic and environmental gradients (Birks, 1995). For some indicators, such as diatoms, the number of lakes required to achieve reliable analogs is currently prohibitive. Furthermore, as is true for all inference models, the training set must be of comparable quality and taxonomy. Constructing large training sets is time consuming if smaller training sets are combined, and few training sets of this nature currently exist (Birks, 1995). Nevertheless, with the creation of larger, combined training sets for the less species rich scaled chrysophytes, we suggest that MAT can now be used as an alternative to regression-based techniques for reconstructing past environments.

Inferring the pH of modern and fossil samples

The intra-, inter-regional, and MAT reconstruction models were used to infer the pH of 53 modern and 48 fossil samples from lakes in south-central Ontario. To simplify

comparisons, the best models from the 53-lake and 117-lake training sets were used. In other studies, where there was no obvious optimal model (e.g. Walker et al., 1997), inferences have been made from several models, and then combined into a single reconstruction. In this study, due to the short DCCA gradient length when constrained solely to pH (Table 1), we determined that unimodal regression-models were not appropriate for the intra-regional data set. Therefore, the linear-based PLS model (2 components) was selected for reconstructing pH. The DCCA gradient length of the inter-regional training set was greater than two SD units, indicating that a unimodal model was more appropriate than the linear-based methods (Table 1). WA-PLS was the best inter-regional model, outperforming the WA models when used to infer the modern pH of lakes in south-central Ontario.

Jack-knifed coefficients of determination and residual structures were examined from comparisons of measured and predicted pH of the south-central Ontario lakes. The 53-lake PLS and 117-lake WA-PLS models showed a strong relationship between the measured and inferred values (Figure 4a, 4b). Surprisingly, the MAT model, which had the highest jack-knifed coefficient of determination and lowest prediction error when developed with the 117-lake training set, did not perform as well as the regression-based models (Figure 4c). Due to its dependence on the size and composition of the training set, MAT predictions could be improved by using a larger data set. For example, when the 117-lake training set was increased to 270 lakes, the relationship between measured and predicted pH improved from r^2_{jack} of 0.59 to 0.69. The larger training set, however, was strongly skewed to the upper end of the pH gradient resulting in overestimates of the

measured values, and so the results of the larger model are not shown here.

An examination of residual structures revealed that the WA-PLS model overestimated the pH of the modern samples. This may have been due to differences in the gradient lengths of the two models, which resulted in higher estimates of taxa optima using the 117-lake model. For example, other studies have consistently reported the pH optimum of *Synura curtispina* to be greater than 7.3 (Dixit et al., 1989b; Cumming et al., 1992; Dixit et al., 1999). Using WA, the estimated optima for this taxon from the 53-lake and 117-lake training sets were 6.9 and 7.4, respectively.

There were strong correlations between the 53-lake PLS model and each of the 117-lake WA-PLS and MAT models, when inferring present-day pH $r = 0.93$, and 0.84, respectively) (Figure 5a). In contrast, correlations of pH inferences for the fossil samples were weaker, with the strongest relationship existing between the PLS and WA-PLS models $r = 0.73$) (Figure 5b). Furthermore, the 117-lake models inferred a higher pH for most fossil samples than the intra-regional model. In part, this may be due to the presence of taxa that were not well represented in the modern training sets. For example, the pH optimum of *Mallomonas allorgei,* estimated from the 53-lake and 117-lake training sets, differed by approximately one pH unit across models, and was higher in the 117-lake data set. As a result of differences in the reconstruction of fossil pH, the WA-PLS and MAT models showed a larger decrease in pH since pre-industrial times (Figure 5c). A total of 54% and 52% of the lakes showed an acidifying trend using the WA-PLS and MAT models, respectively. The PLS model determined that 83% of lakes had increased in pH since pre-industrial times, with 67% showing increases greater than the

$RMSEP_{jack}$ of the model. These discrepancies are of interest to lake managers who must decide which model to believe, and therefore the validation of these reconstructions is essential. Below, we discuss the use of indirect validation techniques that can be used to evaluate the reliability of the inferred pH values.

Validating the pH reconstructions

The most powerful means of validating paleoenvironmental reconstructions is to compare the inferred values with measured water chemistry (Birks, 1998). As historical records of pH were not available for these lakes, we used two indirect numerical criteria. First, bootstrapped error estimates were calculated for each modern and fossil sample. Using the 53-lake model, 27 of the 48 fossil samples were found to have estimated errors of prediction greater than the 95% confidence limit of the distribution of modern errors. In contrast, only one fossil sample had an error larger than the distribution of modern errors when the 117-lake models were used. Second, analog statistics indicated that 18 of the 48 fossil samples had poor modern analogs in the 53-lake training set, 14 of which had also failed the first criterion. Four fossil samples were considered to have poor modern analogs in the inter-regional models.

The above criteria strongly suggest that reconstructions using the intra-regional model are less reliable than either the inter-regional, or MAT inferences. The existence of poor analogs suggests that the taxa present in the fossil samples were poorly represented in the 53-lake training set. This problem was overcome using the inter-regional training set, as a greater number of modern samples provided better analogs for

fossil assemblages. A potential disadvantage of the 117-lake models is that they tend to overestimate the pH of lakes in south-central Ontario. The longer gradient length in the inter-regional training set may have allowed for estimations of taxa optima greater than the pH range of lakes in south-central Ontario.

MAT showed greater variability than the WA-PLS model, resulting in a larger mean bias. Larger biases using MAT have been found in other studies (Birks, 1998), and may result when poor modern analogs exist for fossil samples, or in cases where multiple close analogs exist, but from different environments. Furthermore, MAT models often show greater short-term variability in the record caused by their over-dependence on the range and composition of the modern training set (Bartlein & Whitlock, 1993). Nevertheless, the models show a relatively good correlation $r = 0.64$, $p < 0.001$) of inferred pH change, suggesting that either model could be used to reliably estimate the pH of lakes in south-central Ontario.

In conclusion, we suggest that the 53-lake PLS model cannot be used to reliably reconstruct the pH of fossil samples in south-central Ontario lakes. While the model provided the best estimates of modern pH, approximately half of the fossil species assemblages were found to have poor analogs in the modern samples. WA-PLS and MAT models developed using a 117-lakes training set from south-central Ontario, Adirondack Park, and northeastern USA provide an alternative to the 53-lake PLS model. Finally, we suggest that the WA-PLS model is the most satisfactory model overall, as it generally did not suffer from a poor analog problem, and was less variable than the MAT model.

Acknowledgements

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Table 1. Comparison of intra- and inter-regional training sets, including the gradient lengths of the first DCA axis and the first DCCA axis constrained to pH.

	Intra-regional model	**Inter-regional model**
number of samples	53	117
number of taxa	25	34
minimum pH	5.6	4.5
maximum pH	7.3	8.5
mean pH	6.6	6.5
DCA gradient length (SD)	1.44	3.14
DCCA λ_1	0.09	0.30
DCCA gradient length (SD)	1.07	2.23
species-environment correlation	0.89	0.90

Table 2. Summary of the number of occurrences, and maximum abundances of taxa included in the intra- and inter-regional training sets.

	Intra-regional training set (53 lakes)		Inter-regional training set (117 lakes)	
Taxon	# of occurrences	Max. abundance	# of occurrences	Max. abundance
Chrysodidymus synuroides	–	–	30	12
Chrysosphaerella spp	52	36	74	56
Mallomonas acaroides f. *muskokana*	21	7	67	29
M. akrokomas	34	2	26	2
M. allorgei	9	4	22	25
M. alpina	47	6	21	50
M. caudata	53	20	102	95
M. crassisquama	53	24	88	47
M. duerrschmidtiae	52	43	83	86
M. elongata	36	3	43	5
M. hamata	50	15	93	49
M. heterospina	20	2	26	2
M. hindonii	–	–	27	70
M. insignis	–	–	7	10
M. lelymene	7	2	7	2
M. MEDIUM	35	3	48	11
M. peronoides	–	–	2	6
M. pseudocoronata	52	34	62	64
M. pugio	–	–	2	9
M. punctifera	27	3	64	17
M. SMALL	51	9	95	27
M. torquata	49	3	73	8
M. transsylvanica	–	–	26	4
Paraphysomonas spp	32	2	25	5
Spiniferomonas spp	49	3	33	3
Synura curtispina	40	14	54	47
S. echinulata	52	51	106	65
S. lapponica	–	–	4	3
S. mollispina	–	–	15	49
S. petersenii	53	72	98	80
S. sphagnicola	47	68	85	80
S. spinosa	52	18	73	60
S. spinosa f. *longispina*	–	–	3	9
S. uvella	45	33	53	33

Table 3. Comparison of the performance of the intra-, inter-regional, and Modern Analog Technique (MAT) inference models for reconstructing pH. Apparent and jack-knifed statistics are reported for the regression-based models.

	PLS[1]	WA (clas)[2]	WA (inv)[2]	WAPLS[1]	MAT[3]
Intra-regional training set					
Apparent r^2	0.88	0.82	0.82	0.88	--
Jack-knifed r^2	0.80	0.78	0.77	0.81	--
Apparent RMSE	0.16	0.22	0.20	0.16	--
Jack-knifed RMSEP	0.21	0.23	0.22	0.20	--
Jack-knifed mean bias	0.006	0.006	0.004	0.011	--
Inter-regional training set					
Apparent r^2	0.84	0.83	0.83	0.87	--
Jack-knifed r^2	0.75	0.81	0.81	0.83	0.86
Apparent RMSE	0.45	0.52	0.47	0.40	--
Jack-knifed RMSEP	0.57	0.54	0.50	0.47	0.38
Jack-knifed mean bias	-0.019	-0.010	-0.010	-0.004	-0.049

[1]PLS and WAPLS models are with 2 components.
[2]WA models were calculated without tolerance downweighting.
[3]MAT model was estimated using the mean of the four most similar samples.

Figure captions

Figure 1. The distribution of lakes in the inter-regional training set with respect to pH. Open, cross-hatched, and closed bars represent lakes from south-central Ontario (Hall & Smol, 1996), Adirondack Park (Cumming et al., 1992a), and the northeastern USA (Dixit et al., 1999), respectively.

Figure 2. Relationship between measured pH and DCA Axis 1 for the intra- (53 lakes) and inter-regional (117 lakes) training sets.

Figure 3. Summary of jack-knifed r^2 and RMSEP values from a comparison of observed and predicted pH values, as inferred using the modern analog technique (MAT) model. The predicted pH was estimated from one to ten of the closest analogs. Analysis was performed on square-root transformed species data, using the Bray and Curtis Dissimilarity Measure (Bray & Curtis, 1957).

Figure 4. Relationship between measured and predicted pH, and the residual structures, for modern samples from 53 lakes in south-central Ontario. Comparisons were made using each of the three models: 53-lake PLS, 117-lake WA-PLS, and 117-lake MAT. Squares represent samples with poor analogs, as assessed using analog matching. Diagonal lines represent 1:1 lines.

Figure captions (continued)

Figure 5. Inferred pH values for modern and fossil samples, and the pH change from 48 lakes in south-central Ontario. Pairwise comparisons were made between each of the three models: 53-lake PLS, 117-lake WA-PLS, and 117-lake MAT. Squares represent samples with poor analogs, as assessed using analog matching. Diagonal lines represent 1:1 lines.

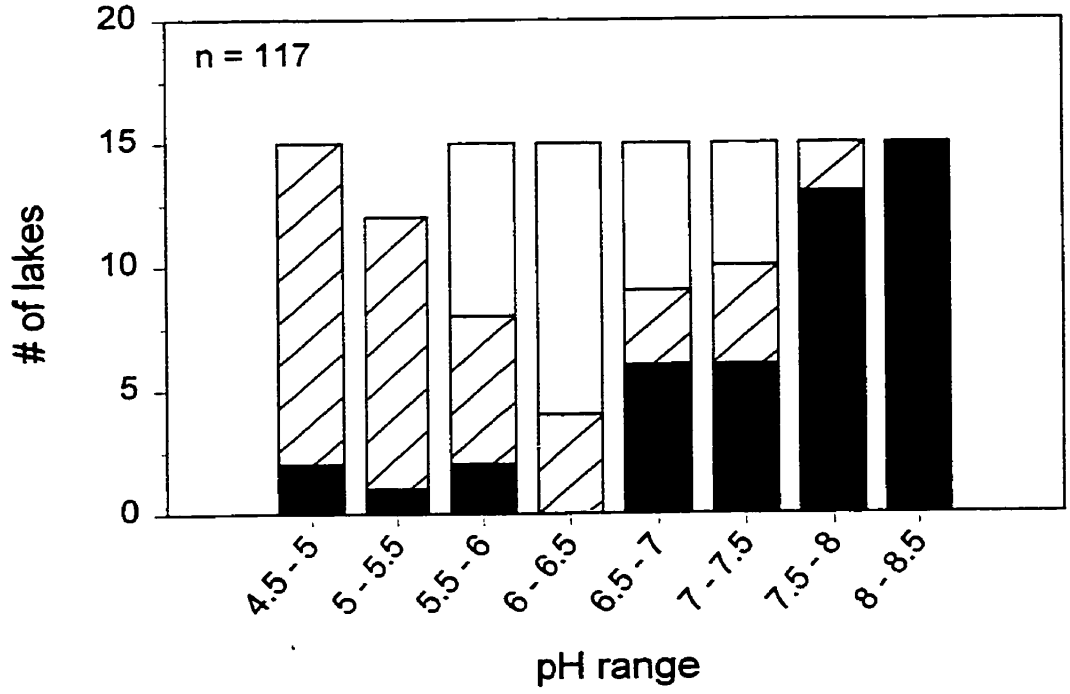

20
15
10
5
0
n = 117
# of lakes
4.5 - 5
5 - 5.5
5.5 - 6
6 - 6.5
6.5 - 7
7 - 7.5
7.5 - 8
8 - 8.5
pH range

Figure 1

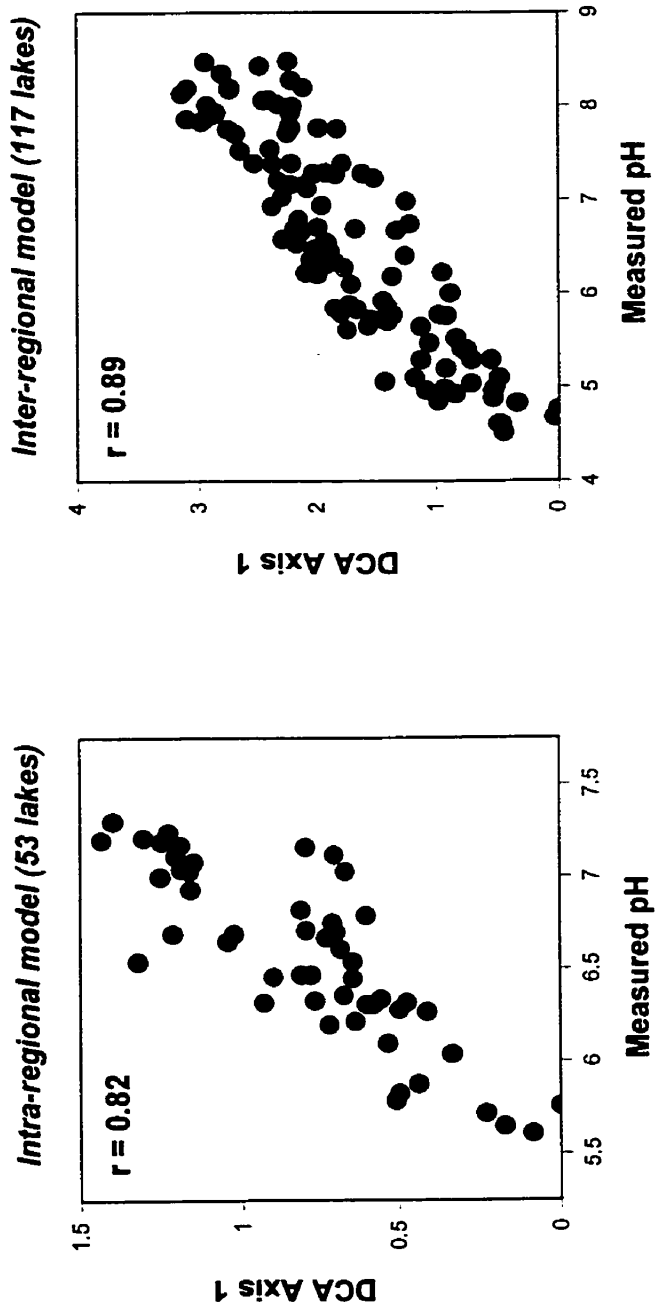

Inter-regional model (117 lakes)
r = 0.89
DCA Axis 1
Measured pH
Intra-regional model (53 lakes)
r = 0.82
DCA Axis 1
Measured pH

Figure 2

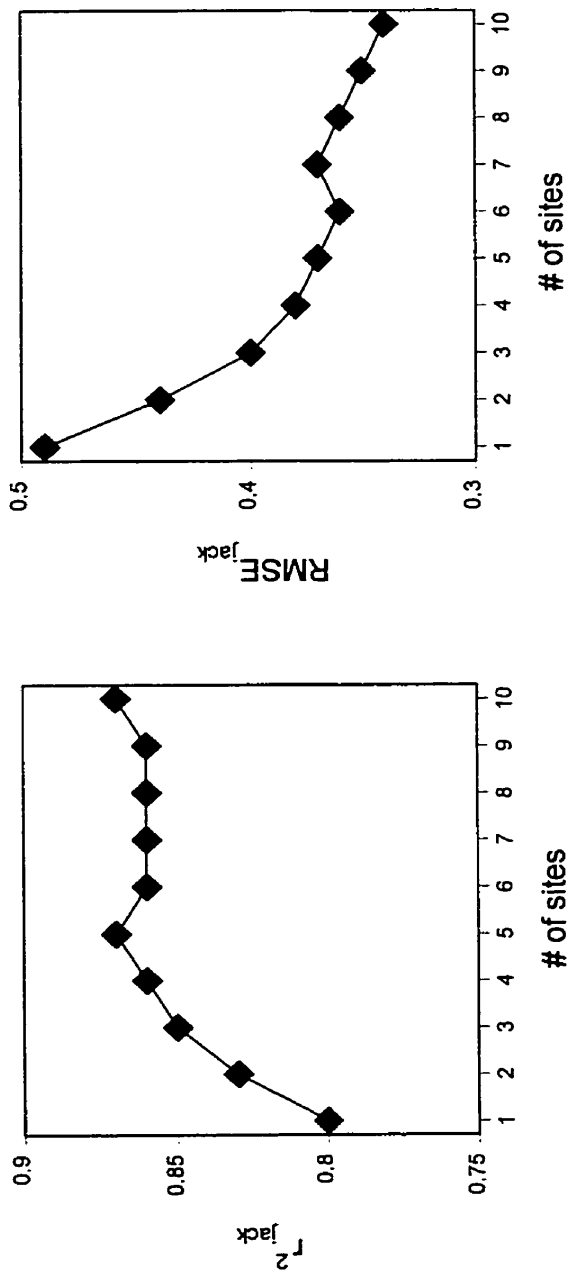
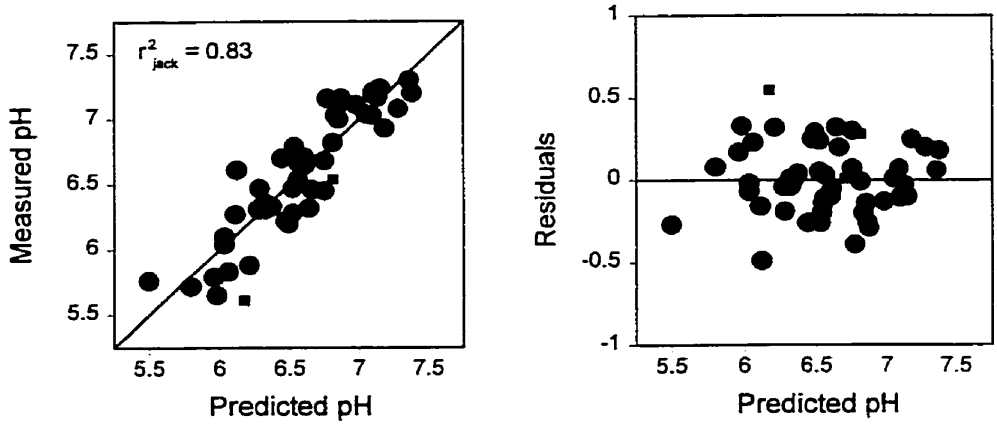
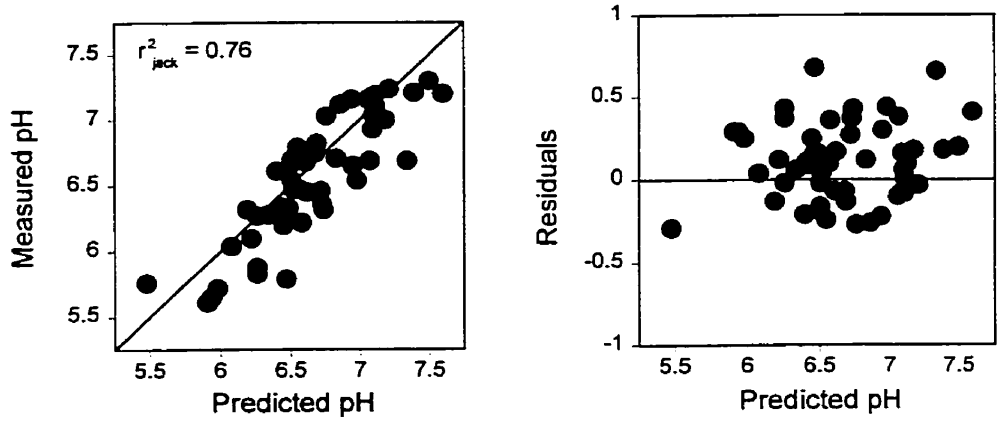

RMSE jack
0.5
0.4
0.3
1 2 3 4 5 6 7 8 9 10
# of sites
r2 jack
0.9
0.85
0.8
0.75
1 2 3 4 5 6 7 8 9 10
# of sites

Figure 3

a) 53-lake PLS model



b) 117-lake WAPLS model



c) 117-lake MAT model

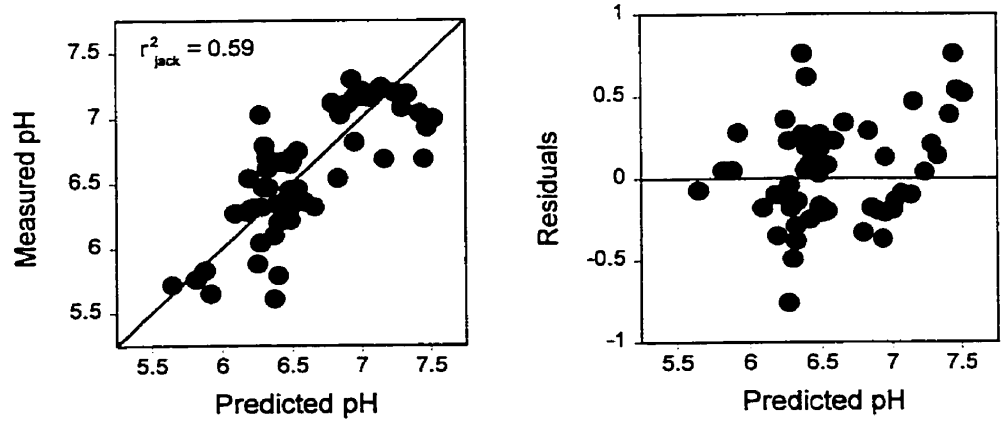
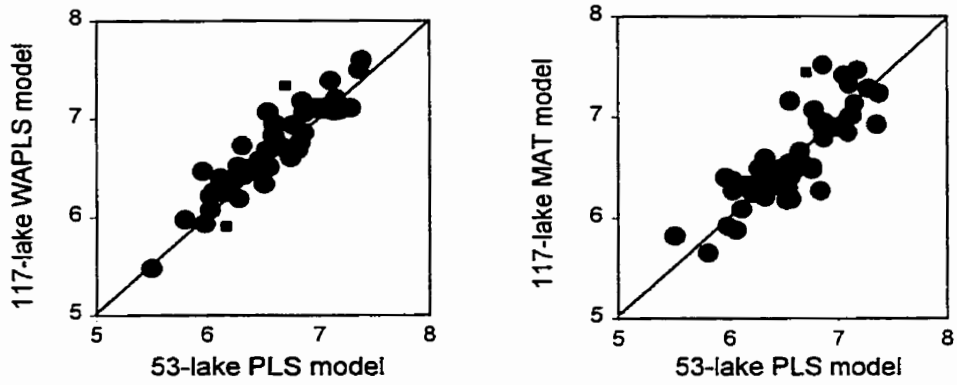
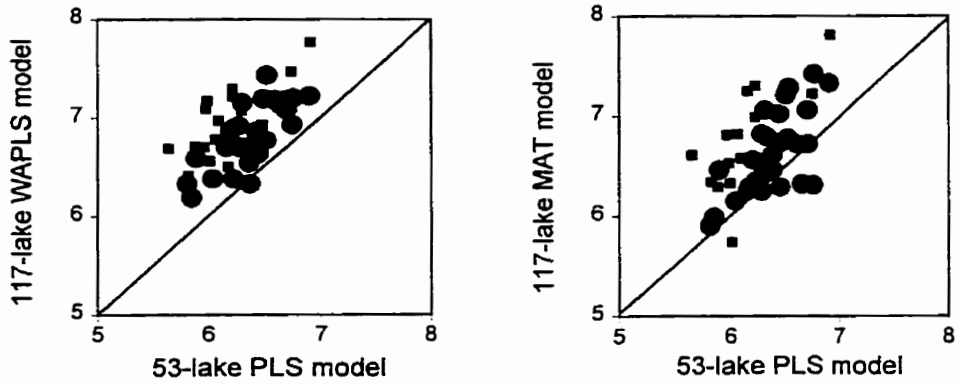


Figure 4

a) Modern samples: Inferred pH



b) Fossil samples: Inferred pH



c) Inferred change in pH

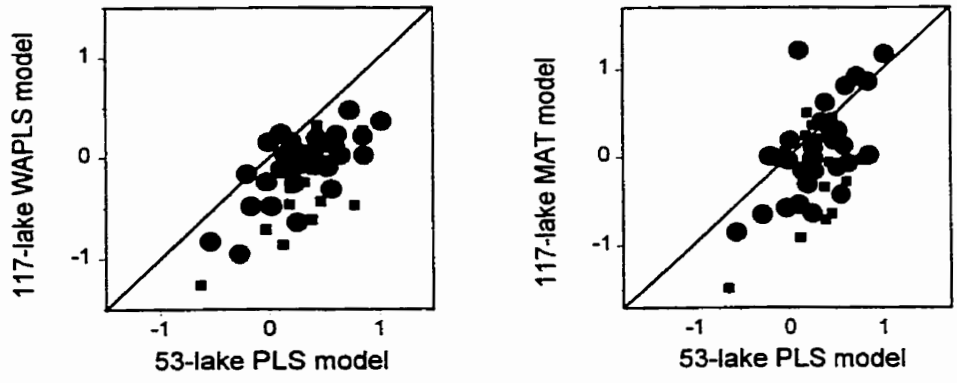


Figure 5

CHAPTER 4

SCALED CHRYSOPHYTES AS PALEOLIMNOLOGICAL INDICATORS OF WATER QUALITY CHANGES IN SOUTH-CENTRAL ONTARIO LAKES AFFECTED BY ACIDIC DEPOSITION

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Abstract

Scaled chrysophytes preserved in 53 present-day and 48 pre-industrial sediment samples from lakes in south-central Ontario were examined to evaluate changes in water quality since pre-industrial times. The relationship between modern species assemblages and measured environmental variables was explored using the constrained ordination technique, redundancy analysis. The distribution of chrysophyte taxa was related to a primary gradient of pH, alkalinity and ion concentration ($\lambda_1 = 0.26$), and a secondary gradient of DOC and nutrients ($\lambda_2 = 0.12$). A combined, 117-lake reconstruction model from Ontario, the Adirondacks, and northeastern USA was used to infer the lakewater pH of present-day (top) and pre-industrial (bottom) samples. A comparison of the predicted and measured pH of modern samples, analog matching, and an examination of inferences from triplicate cores in four lakes, suggested that the pH inferences were reliable. All of the lakes with measured pH < 6, and 63% of lakes with a pH < 6.5, showed a decline in pH since pre-industrial times. In contrast, 71% of lakes with a measured pH > 7 increased in pH. However, in comparison to other acid-sensitive regions, the overall change was small in these lakes. The relatively short pH gradient, comparatively higher pre-industrial pH values, and the amount of acid deposition are factors that may explain these trends. Finally, we introduce a new, multi-indicator reconstruction model that can be used to interpret changes in lakewater pH in the Muskoka-Haliburton region. We discuss how this model, which provides an average of environmental reconstructions from diatom, chrysophyte cyst, and scaled chrysophyte inference models, may be of particular interest to lake managers.

Introduction

Muskoka-Haliburton is located within the Canadian Precambrian shield, approximately 200 km north of Toronto, Ontario (Fig. 1). Since the mid-19th century, the water quality of Muskoka lakes has been increasingly threatened by anthropogenic disturbances. These disturbances occur both at a watershed-scale, such as the input of nutrients from septic systems (Dillon and Rigler 1975; Dillon et al. 1993), and at a regional-scale, including the deposition of strong acids from long-range transport (Dillon et al. 1987; Stoddard et al. 1999). Disentangling the relative effects of these factors on water quality is complicated because they may act synergistically in many lakes. Furthermore, changing climatic conditions can play a confounding role (e.g. Schindler et al. 1996; Yan et al. 1996). Despite growing evidence that water quality may be adversely affected by these disturbances, few studies have attempted to quantify these effects relative to background or pre-industrial conditions.

The processes controlling the acidification and recovery of lakes in south-central Ontario are complex. Despite a decline of 35-40% in the deposition of sulphate in the region, the response in lakes has been variable (Dillon and LaZerte 1992; Stoddard et al. 1999). McNicol et al. (1998) reported that the majority of 216 small, acid-sensitive lakes in the Muskoka region of Ontario showed no change in pH following the reduction in deposition. In part, these trends may be the result of a depletion of cations from watershed soils from decades of acidic deposition (Likens et al. 1996). The re-oxidation and release of reduced sulphur stored in wetlands has also been recognized as a contributing factor delaying the recovery of acidified lakes (Yan et al. 1996), which may

be linked to abnormally dry periods, such as years following El Niño events (Dillon et al. 1997*b*).

Long-term data and a knowledge of pre-disturbance conditions are required to assess the effects of environmental stressors on water quality (Smol 1992). Historical records and monitoring programs provide direct measurements and are preferred sources of such data, but are rare or non-existent in many regions. In the Muskoka-Haliburton region of south-central Ontario, more than twenty-five years of continuous monitoring has provided insight into the impacts of anthropogenic disturbances on the hydrology and ecology of Canadian Shield lakes (e.g. Dillon et al. 1987). However, even these programs are not long enough to provide information about environmental conditions prior to the onset of many perturbations (e.g. acidification). This problem may be overcome through the implementation of paleolimnological techniques, which use information that is archived in the sediment record to reconstruct past environments (Smol 1992).

The top-bottom paleolimnological approach may be used to obtain regional estimates of environmental change since pre-industrial times. Biological assemblages that are preserved in the surface sediments of lakes (top samples) are compared with those from pre-industrial (i.e. pre-1850s) samples (bottom samples), providing a measure of environmental change relative to background or 'natural' conditions. The top-bottom technique has been used successfully to infer changes in water quality variables (e.g. pH, alkalinity, heavy metals, total phosphorus) in many regions of North America, including Sudbury, Ontario (e.g. Dixit et al. 1992*b*), and the Adirondacks, NY (e.g. Sullivan et al.

1990; Cumming et al. 1992*a*), as well as in other regions (e.g. Sweden: Korsman 1999). Recently, top-bottom paleolimnological studies in the Muskoka-Haliburton region have been used to infer changes in lake water pH, total phosphorus (diatoms: Hall and Smol 1996; chrysophyte cysts: Wilkinson et al. 1999), and lakewater oxygen (chironomids: Quinlan et al. 1998). Results from these studies suggest that changes in water quality have been minimal in many of the Muskoka lakes. For example, Hall and Smol (1996) and Wilkinson et al. (1999) determined that 60% and 70% of lakes, respectively, had not changed significantly in pH and total phosphorus since pre-industrial times.

Using multiple indicators in paleolimnological studies may provide a more complete understanding of environmental change. Scaled chrysophytes are sensitive indicators of changes in water quality (Smol 1995). These planktonic organisms are important components of the phytoplankton of lakes in the Precambrian shield (Sandgren 1988; Siver 1995). The siliceous scales and bristles of scaled chrysophytes are often abundant and well preserved in lacustrine sediments (Smol 1995). Using a light microscope, the scales from many taxa may be reliably identified to the species or sub-species level. Individual taxa have been shown to have well-defined ecological optima and tolerances that can be quantitatively modelled to infer environmental conditions in the past (Siver 1995). For example, the distribution of chrysophyte taxa may be influenced by many variables, including lake water conductivity (Siver 1993*a*), total phosphorus (Siver 1991), and temperature (Siver 1995). Lakewater pH, however, has been shown to be the primary physical-chemical variable influencing scaled chrysophyte assemblages in many of these studies (e.g. Cumming et al 1992*a*; Dixit et al. 1992*b*; Dixit

et al. 1999). Since the early 1980s (Smol et al. 1984), paleolimnological studies have used scaled chrysophytes as indicators of lake acidification in many regions of North America (e.g. Cumming et al. 1994; Dixit et al. 1990, Dixit et al. 1992*a*).

In this paper, we explore changes in water quality since pre-industrial times in Muskoka-Haliburton lakes, using scaled chrysophytes as indicators of environmental change. First, ordination techniques are used to explore the relationship between scaled chrysophyte assemblages and measured environmental variables from 53 lakes in south-central Ontario. Gaining an understanding of the ecological preferences of chrysophyte taxa along environmental gradients is an important first step in interpreting changes in water quality. Second, we explore regional trends in lakewater pH since pre-industrial times. Monitoring studies in the Muskoka-Haliburton region suggest that many lakes have been adversely affected by the deposition of strong acids (e.g. Stoddard et al. 1999). However, the paleolimnological evidence suggests that these impacts have been small since pre-industrial times (Hall and Smol 1996, Wilkinson et al. 1999). Scaled chrysophytes provide an additional interpretation of changes in pH in these lakes. These organisms have been shown to be sensitive indicators of lake acidification (Smol 1995), often showing inferred pH changes greater than those from other indicators (e.g. diatoms). Finally, we introduce a new, multi-indicator reconstruction model that may be used to better understand changes in lakewater pH in the Muskoka-Haliburton region. We discuss how this model, which incorporates information from diatom (Hall and Smol 1996) and chrysophyte (Wilkinson et al. 1999; this study) inference models, may be of particular interest to lake managers.

Methods

Study region

The Muskoka-Haliburton region of south-central Ontario is underlain by Precambrian granitic bedrock of the Canadian Shield (Jeffries and Snyder 1983). A marble intrusion, found in the eastern portion of the study area, underlies twelve of the study lakes. Soils are generally shallow and acidic, although thicker deposits of clay, sand, or gravel occur locally (Chapman and Putnam 1984). Much of this region is characterized by secondary mixed-deciduous and coniferous forests, following widespread deforestation in the mid- to late-1800s (Michalski et al. 1973). Due to the rough topography, thin soils, and cool climate, agriculture is marginal in the region. Presently, human activity consists primarily of recreational activities associated with seasonal cottages, and rural municipalities.

Field and laboratory work

In the fall of 1992, 54 lakes in the Muskoka-Haliburton region were selected for study (Hall and Smol 1996) (Table 1). Sediment cores were extracted from the deepest basin of each lake using a Glew (1989) gravity corer fitted with a 6.35-cm internal diameter Lucite tube, and sectioned at the lakeshore into stratigraphic sections using a Glew (1988) vertical extruder. Two sediment sections were examined: the top centimetre (present-day lake conditions), and a 1-cm interval taken at a minimum core depth of 20-cm (pre-industrial lake conditions). Although the precise date of the bottom sample of each core is not known, radiometric ^{210}Pb-dating of other cores from the south-central Ontario

region has shown that background conditions (i.e. > 150 years) are typically reached at core depths of 15-20 cm (e.g. Clerk et al. 2000; Dixit et al. 1990; Dixit et al. 1992*a*).

Water chemistry data were collected from 1990 to 1992 by personnel of the Ontario Ministry of the Environment (Hall and Smol 1996). All variables, excluding total phosphorus, were calculated as volume-weighted averages of ice-free concentrations for this time period. Total phosphorus measurements were calculated as spring overturn values. Morphometric variables, including maximum depth (Zmax), surface area (SA), watershed area (WA), and a volume-weighted measure of lakeshore development (# of cottages.SA^{-1}.Zmax) were also calculated (Wilkinson et al. 1999), bringing the total number of physical-chemical variables to eighteen (Table 2).

Microscope slides were prepared following the standard acid-digestion techniques described in Hall and Smol (1992). A minimum of 300 chrysophyte scales were enumerated along transects at 1500X (100X objective, 15X ocular lens) using a Leica DMRB light microscope with differential-interference-contrast optics. Taxonomic identification of scales followed Siver (1991, 1993*b*), Takahashi (1978), Wee (1982), Kling and Kristiansen (1983), Nicholls (1982, 1988), and a reference collection at the Paleoecological Environmental Assessment and Research Laboratory, Queen's University. Scales of a few taxa were grouped into broader taxonomic categories because of difficulty in identifying these scales to the species level using a light microscope. For example, unidentifiable small and mid-sized scales were grouped into the categories *Mallomonas* 'small' and 'medium', respectively. These groups were relatively rare, with abundances of no greater than three or six percent in any lake.

Statistical analysis

In total, 32 taxa were identified in the top and bottom sediment samples of the study lakes. Eight taxa were considered rare as they did not reach a relative abundance of greater than 1% in any sample, and were eliminated from subsequent analyses (Table 3). For statistical analyses, species data were square-root transformed to reduce the impact of very abundant taxa (e.g. Cumming and Smol 1993). Detrended correspondence analysis (DCA), with detrending by segments, was used to determine the maximum amount of variation in the species data (Hill and Gauch 1980). Due to the short gradient length of the first DCA axis (1.44 standard deviation units), linear ordination techniques were used to determine the main directions of variation in the chrysophyte data (principal components analysis), and to explore the relationship between scaled chrysophyte assemblages and the eighteen environmental variables (redundancy analysis).

A forward selection step was used with redundancy analysis (RDA) to reduce the problem of co-linearity in the explanatory variables. Environmental data were screened for normality, and log or square-root transformed if appropriate, to meet the assumptions of parametric statistical analyses. Monte Carlo permutation tests (999 permutations) were used to: 1) test the significance of each forward selected variable, and 2) test the significance of the first and second RDA axes defined by the forward selected environmental variables. The statistical package CANOCO version 4 (ter Braak and Smilauer, 1998) was used for the ordinations.

Variance partitioning (Borcard et al. 1992) was used to determine the importance of chemical variables and spatial structure (calculated as Cartesian coordinates: x, y, x^2,

y^2, x^2y, xy^2, from latitude and longitude values), in addition to their interaction. Two RDA's constrained to forward chemical variables (pH, DOC, log[Na], $[SO_4]$, log$[NH_3]$, and $[NO_3]$), and spatial (y^2, x^2y, xy^2) variables, to determine the variance explained by these groups. The co-variance explained by chemical and spatial variables was estimated (see Borcard et al. 1992). This was calculated from the total variance explained by the chemical variables minus the variance explained when spatial variables were included as co-variables (Borcard et al. 1992).

The pH of modern and fossil samples was inferred using a 117-lake reconstruction model, which included lakes from this study (Hall and Smol 1996), Adirondack Park (Cumming et al. 1992a), and northeastern USA (Dixit et al. 1999). The 117-lake model was used in place of an intra-regional model developed using the 53 lakes in south-central Ontario. The 53-lake model was found to be unreliable when reconstructing the pH of fossil samples, as many had species assemblages that were not well represented in the modern samples (Chapter 3). A strong relationship between measured pH and detrended correspondence analysis (DCA) axis one scores ($r = 0.89$) determined that pH tracked the main direction of variation in the 117-lake training set. Detrended canonical correspondence analysis (DCCA), with pH as the sole constraining variable, suggested that unimodal modelling techniques were appropriate for inferring the pH of modern and fossil samples (Chapter 3). A weighted averaging partial least squares (WA-PLS) regression and calibration model (2 components) was used to reconstruct the pH of south-central Ontario samples, using the program CALIBRATE (S. Juggins & C.J.F. ter Braak,

unpublished program).

Variability as a result of sampling, counting and random errors may influence the reconstructions in this study (Cumming et al. 1990). A number of tests were performed to assess the reliability of the pH inferences. First, the 117-lake model was used to predict the pH of the modern samples. The jack-knifed coefficient of determination and residual structure of the comparison were examined. Second, analog matching was applied to determine whether fossil species assemblages were well represented in the modern samples of the 117-lake training set. Using the Bray-Curtis coefficient (Bray and Curtis 1957), a distribution of minimum dissimilarities was calculated through comparisons among modern samples. When compared to modern samples, fossil samples with minimum dissimilarities greater than the extreme 5% of modern distribution were considered to have poor analogs. Analog matching was performed using the statistical program ANALOG version 1.6 (J.M. Line and H.J.B. Birks, unpublished program). Third, triplicate cores were collected from the deepest basin of four of the lakes [Bass (2), Crosson (13), Dickie (14), and Little Clear (34)]. Top and bottom samples were enumerated for each of the cores, and pH inferences were compared.

To test whether species changes were related to changes in pH, a Bray-Curtis dissimilarity was calculated between the modern and fossil sample of each lake, and compared to the absolute value of the inferred pH change. Lakes that had both a: 1) Bray-Curtis dissimilarity greater than the mean value (0.41), and 2) pH change less than the mean change (0.28 pH units), were considered to be outliers. These lakes exhibited

species changes that were not strongly related to changes in pH.

A single, multi-indicator reconstruction model for inferring lakewater pH was calculated by combining the diatom (Hall and Smol 1996), chrysophyte cyst (Wilkinson et al. 1999), and scaled chrysophyte (this study) inferences of pH in two ways: 1) a mean weighted by the cross-validated coefficient of determination (r^2) of each model, which was calculated from comparisons of predicted and observed pH, and 2) a mean weighted by one minus the cross-validated prediction error (RMSE), which was calculated separately for each paleolimnological indicator. The performance of the multi-indicator models was evaluated by comparing the predicted inferences of the modern samples with measured values.

Results and Discussion

A total of 32 scaled chrysophyte taxa or groups were identified in the surface sediment of the study lakes. Chrysophyte scales were extremely rare in the surface sediment of Three Mile Lake, and therefore this lake was excluded from further analyses. In general, the present-day sediment samples were dominated by taxa of the genus *Synura*. In 41 of the 53 lakes examined, the relative abundance of *Synura* taxa was greater than 50%. *Synura* accounted for greater than 75% of the species assemblage in 16 of the lakes. The most abundant chrysophyte taxon in the modern samples was *S. petersenii*, occurring at an average relative abundance of 28% across all lakes, and reaching relative abundances of greater than 30% in 20 of the lakes. *S. sphagnicola* and *S. echinulata* also contributed to the high total *Synura* abundances, with average relative

abundances of 14% and 8%, respectively. By comparison, the most abundant *Mallomonas* taxa in the surface samples were *M. crassisquama* and *M. duerrschmidtiae*, with average relative abundances of 9% and 7%, respectively.

Chrysophyte scales were extremely rare in five fossil samples [Bruce (7), Butterfly (9), Frazer Island (16), Heney (25), and Plastic (42)], and therefore top-bottom comparisons were not possible for these lakes. A comparison of modern and fossil sediment intervals suggested that there has been a regional shift from a *Mallomonas* to a primarily *Synura*-dominated species assemblage (Fig. 2a, 2b). *M. duerrschmidtiae* and *M. crassisquama* were the most abundant taxa in the pre-industrial time period, occurring at mean relative abundances of 26% and 15% across all lakes (Fig. 2b). *S. petersenii*, the most abundant *Synura* taxon in both the present-day and pre-industrial time periods, was found at a mean relative abundance of approximately 8% in the fossil samples (Fig. 2a).

The relationship between scaled chrysophytes and environmental variables

Eigenvalues ($\lambda_1 = 0.31$, $\lambda_2 = 0.19$) of the first and second PCA axes accounted for 50.2% of the variation in the species data. The strength of the first axis suggested that the distribution of chrysophyte taxa in the modern samples was related to a strong primary gradient. In an exploratory RDA, including all of the measured environmental variables, the first ($\lambda_1 = 0.28$) and second ($\lambda_2 = 0.14$) axes explained 42.1% of the cumulative variance in the species data. Forward selection found six environmental variables (pH, DOC, log[Na], [SO_4], log[NH_3], and [NO_3]) that explained significant directions of variation in the chrysophyte data. Constrained to the forward selected environmental

variables, the eigenvalues of the first ($\lambda_1 = 0.26$) and second ($\lambda_2 = 0.12$) RDA axes were significant ($p \leq 0.01$), and explained 37.9% of the cumulative variation in the chrysophyte data. Species-environmental correlations of the first two RDA axes were high (0.92 and 0.81), suggesting that the forward selected environmental variables explained major directions of variation in the species data.

An examination of the importance of spatial structure on chrysophyte distributions determined that three forward selected spatial variables (y^2, x^2y, xy^2) could significantly explain 16% of the cumulative variance in the chrysophyte data. After the removal of the variance shared with the forward selected chemical variables, the variance explained by space alone was reduced to 9%, considerably less than the variance unique to the chemical variables alone (35%). Given the small amount of variance accounted for by space alone, in comparison to the importance of the chemical variables, we only discuss the latter in detail.

The RDA axis 1 captured a gradient of pH and pH-related variables (Table 4, Fig. 3). Alkalinity, conductivity, and ionic concentration ([Mg], [K], [Ca], and [SO_4]) were highly correlated with pH along the first axis (Fig. 3a). RDA axis one effectively separated low conductivity, acidic lakes [Fig. 3c: Chub (11), Clear (12), Crosson (13), Dickie (14), Heney (25), and Plastic (42)], from some of the more alkaline lakes [Fig. 3c: Eagle (15), Moose (39), and Oblong (41)]. All of the lakes found within the marble inclusion were clustered towards the more alkaline end of the first RDA axis (Fig. 3c). When dissolved with acid precipitation, the marble provides a source of $CaCO_3$, thereby increasing the buffering capacity of these lakes.

Similarly, chrysophyte taxa that commonly occur at higher relative abundances in more acidic environments (Siver 1995), such as *Mallomonas acaroides* v. *muskokana* and *Synura sphagnicola*, were positioned at the acidic end of the pH gradient (Fig. 3b; Fig. 4). *M. hindonii*, an excellent indicator of low pH (e.g. Cumming et al., 1992a), did not meet the abundance criteria in these lakes, and therefore was not included in the ordinations (see Methods). The *Synura* species, *S. uvella* and *S. curtispina*, were positioned at the alkaline end of the first RDA axis (Fig. 3b; Fig. 4). Interestingly, *S. echinulata* was also positioned at the alkaline end of the gradient, despite evidence that this species is largely acidophilous in its preference to pH (Siver 1995). This finding is supported by Cumming et al. (1992*a*) and Dixit et al. (1999), who reported a bimodal response of *S. echinulata* along a gradient of pH from lakes in Adirondack Park, and northeastern North America, respectively. Due to the absence of strongly acidic lakes in this study (Table 2), the more acidophilous form of the taxon may have been under-represented in the lake set. It is possible that the taxon identified here is actually *Synura leptorrhabda* (Asmund) Nicholls comb. nov., which has been shown to occur in south-central Ontario lakes (Nicholls and Gerath 1985). This taxon may only be reliably separated from *S. echinulata* using an electron microscope. Previous reports of this taxon have given little indication regarding its ecological preferences, although it has been shown to occur in lakes within the Canadian Shield (Kling and Kristiansen 1983).

The importance of pH to the distribution of scaled chrysophytes has been well documented in other studies (Smol 1995). For example, in a study of 71 lakes in the Adirondack Mountains, NY, pH and related variables (e.g. monomeric aluminum) were

found to be important variables influencing the distribution of chrysophyte taxa (Cumming et al. 1992a). A recent, comprehensive study of the relationship of scaled chrysophytes to environmental variables from surface samples of 217 lakes in northeastern, USA, determined that pH was the most important variable influencing species distributions (Dixit et al., 1999). In the south-central Ontario lakes, conductivity was strongly correlated to pH along the first RDA axis, and has been identified as an important variable influencing chrysophyte populations in other studies. Siver (1993*a*) reported a good relationship (apparent $r^2 = 0.87$) between observed and chrysophyte-inferred conductivity values in an analysis of 28 lakes in Connecticut (mean conductivity range: 28-294 μS/cm, with 13 lakes greater than 100 μS/cm). The comparatively narrow gradient of conductivity observed in the Muskoka-Haliburton lake-set (22-87 μS/cm) is too short to obtain meaningful estimates of the ecological optima and tolerances of the chrysophyte taxa.

Gradients of dissolved organic carbon (DOC), trophic variables ([TN] and [TP]so), and morphometric variables (Zmax and COT/SA*Z) were captured by the second RDA axis (Table 4, Fig. 3a). The ordination separated shallow, more productive lakes from deeper, less productive lakes. Furthermore, the second axis separated naturally acidic lakes with higher concentrations of DOC [e.g. Gullfeather (19)] from clear, acidic lakes, that have acidified as a result of anthropogenic influences [e.g. Plastic (42)]. *M. hamata* and *M. duerrschmidtiae* were positioned at the low end of the DOC/nutrient gradient, indicating that these taxa were most common in deeper, oligotrophic lakes (Fig. 3b). This is supported by Siver (1991), who reported these taxa

at higher abundances in oligotrophic or mesotrophic habitats with low total phosphorus. With the exception of *S. spinosa*, *Synura* taxa were more common in shallower lakes, characterized by higher DOC and nutrient levels (Fig. 3b). This was true of taxa independent of their positioning along the pH gradient (e.g. *S. sphagnicola* and *S. curtispina*). Although DOC was highly correlated with trophic variables ([TN] and [TP]so) along the second RDA axis, the data did not allow us to separate the relative importance of DOC and trophic variables to the distribution of chrysophyte taxa.

Assessing the reliability of the pH reconstructions

The pH of the 53 modern and 48 fossil samples was inferred using a 117-lake weighted-averaging partial least squares (WA-PLS) reconstruction model, which included lakes from Ontario (Hall and Smol 1996), Adirondack Park (Cumming et al 1992*a*), and the northeastern USA (Dixit et al. 1999). The WA-PLS model was found to be robust, producing a cross-validated coefficient of determination and prediction error well within the range of other pH models developed using scaled chrysophytes (e.g. Cumming et al. 1992*a*; Dixit et al. 1992*b*). A detailed summary of the development of the WA-PLS model is found in Chapter 3.

To test the ability of the 117-lake model to reconstruct the pH of Ontario lakes, the WA-PLS model was used to predict the measured pH of the 53 modern samples. There was a strong relationship between predicted and measured pH, as inferred using the WA-PLS model (Fig. 5). An examination of the residual structure of the relationship suggested that the 117-lake model tended to overestimate the pH of the Ontario samples.

However, this bias was constant along the pH gradient (Fig. 5), suggesting that reliable inferences of pH change (inferred modern pH - inferred fossil pH) could be made.

A second test of the reliability of the pH inferences was analog matching which determined that only four fossil samples had species assemblages that were poorly represented in the 117-lake training set. The fossil samples of one of these lakes [Clear (12)] was dominated by the chrysophyte *M. allorgei*, a taxon that is poorly represented in modern samples of many regions of North America (Siver 1991). A second poor analog [Solitaire (49)] had an unusual species assemblage co-dominated by *S. uvella* and *M. duerrschmidtiae*, taxa that do not typically occur together in high abundances in either the 53-lake and 117-lake training sets.

A comparison of pH inferences from modern and fossil samples of triplicate cores suggested that the variability among replicates was low (Fig. 6). In two lakes that have shown a significant change in pH since pre-industrial times, the variation between top and bottom inferences was greater than the variation among replicates (Fig. 6). Collectively, these results suggest that pH inferences from scaled chrysophyte assemblages examined in sediment cores extracted from the deep basin of lakes are reproducible (Cumming et al. 1990), and the pH of the Muskoka lakes can be reliably inferred.

In modern training sets, ordination techniques can be used to determine if an environmental variable of interest tracks the main direction of variation in the species data (Birks 1995). However, these comparisons are rarely made with fossil assemblages, and have yet to be used in top-bottom paleolimnological studies. To determine if pH tracked an important direction of variation in the species data through time, we compared

the absolute value of inferred pH change with a measure of species dissimilarity (i.e. Bray-Curtis coefficient). Across lakes, a moderate relationship existed between Bray-Curtis dissimilarities and the inferred pH change ($r = 0.56$, $n = 48$, $p < 0.001$), further validating the pH reconstructions, and suggesting that pH was an important variable related to species changes (Fig.7). However, ten lakes exhibited species changes that were not strongly related to inferred changes in lake water pH (see criteria in Methods) (Fig. 7). The chrysophyte *S. petersenii* dominated the species assemblage of five of these lakes. Interestingly, *S. petersenii* increased in relative abundance in all but four lakes since pre-industrial times, and presently is the most abundant scaled chrysophyte in approximately half of the lakes. The importance of this species as it relates to the water quality of lakes in south-central Ontario is discussed elsewhere (Chapter 5).

Changes in lakewater pH since pre-industrial times

Our findings suggest that changes in lakewater pH have been small in the study lakes. Approximately 80% of the lakes showed pH changes less than the prediction error of the scaled chrysophyte inference model (Fig. 2c). Similar results have been reported using other paleolimnological indicators. For example, greater than 60% of the study lakes showed non-significant pH changes as inferred from both diatom (Hall and Smol 1996) and chrysophyte cyst (Wilkinson et al. 1999) inference models.

Although the magnitude of pH change was not significant (i.e. greater than prediction error of model), there were regional trends with respect to the direction of change in many lakes. For example, of the 10 lakes that had changed significantly since

pre-industrial times, 90% had acidified. All of the lakes with measured pH < 6, and 63% of lakes with a pH < 6.5, showed a decline in pH (Fig. 2c). In contrast, 71% of lakes with a measured pH > 7 increased in pH, although only one lake had increased significantly since pre-industrial times (Fig. 2c). Equal numbers of circumneutral lakes (measured pH 6.5-7) either increased or decreased in pH (Fig. 2c).

Top-bottom paleolimnological studies, using scaled chrysophytes as indicators of environmental change, have reported similar trends in Sudbury, Ontario (Dixit et al. 1992*b*) and the Adirondacks (Cumming et al. 1992*a*). However, the magnitude of change was considerably smaller in south-central Ontario, with only one lake showing acidification of greater than 1 pH unit. In part, this discrepancy may reflect the gradient of lakes examined in the Muskoka study. Very acidic lakes (e.g. measured pH < 5.5), that often show the greatest declines with acid deposition (e.g. Cumming et al. 1992*a*; Dixit et al. 1992*b*), were excluded from this data set, thereby underestimating the extent of overall acidification in this region. Furthermore, inferred values of pre-industrial pH were higher in the Muskoka than the Adirondack lakes, suggesting that the former were comparatively well buffered, and therefore more resistant to acidification (Cumming et al. 1994). Finally, the amount of sulphate deposition, as measured in the early 1980s, has been considerably less in south-central Ontario (Lazerte and Dillon 1984: 70-100 μeq/L) than in the Sudbury region (Keller et al. 1992: > 200 μeq/L), which may have contributed to the smaller inferred changes in the Muskoka lakes (Smol et al. 1998).

Diatom (Hall and Smol 1996), chrysophyte cyst (Wilkinson et al. 1999), and scaled chrysophyte (this study) inference models suggest that study lakes with a measured

pH > 7 have increased in pH since pre-industrial times. In south-central Ontario and in other regions receiving elevated acidic deposition (e.g. Sudbury: Dixit et al. 1992*b*; Adirondacks: Cumming et al. 1992*b*), several mechanisms may have contributed to the observed increases in alkalinity. First, the disturbance or removal of watershed vegetation may increase soil erosion, causing an increase in the export of base cations (e.g. Rhodes and Davis 1995). The removal of forests for timber in the late 1800s, the building of roads, and the construction of seasonal cottages and resorts are disturbances that may have contributed to this process. The importance of these disturbances on the acid-base chemistry of the lakes will be regulated by watershed characteristics (e.g. underlying geology, drainage ratio, catchment slope). For example, more than 85% of the lakes that increased in alkalinity overly a marble intrusion, and are relatively well buffered compared to lakes situated on granitic bedrock (Wilkinson et al. 1999) (Fig. 2c).

Cation exchange, and sulphate and nitrate reduction in watershed soils, wetlands, and lake sediments are other processes that may have contributed to the observed increases in alkalinity in the Ontario lakes (e.g. Dillon et al. 1997*a*; Schindler 1986). These too are regulated by watershed characteristics (e.g. % wetlands), and by changes in climate, which may cause a reversal of these trends immediately following drought (Yan et al. 1996). Without knowing the timing of changes in these lakes, we cannot separate the relative contributions of these mechanisms to alkalinity generation. Analyses of continuous sediment cores will be required to further address these questions.

A multiple-indicator measure of lake acidification in the Muskoka-Haliburton region

At a regional scale, pH inferences from the diatom and chrysophyte models showed similar trends, with greater than 60% of the lakes indicating a non-significant change since pre-industrial times. These similarities were not always apparent at a lake-scale. Scaled chrysophyte and diatom models showed moderate agreement ($r = 0.56$, $n = 48$, $p < 0.001$) across lakes in inferring changes in lakewater pH (Fig. 8). In general, scaled chrysophytes inferred a greater decrease in pH, which may reflect organism-specific differences in habitat and life history (see below). Inferences derived from chrysophyte cysts showed little agreement with the scaled chrysophyte ($r = 0.00$, $n = 48$, $p > 0.05$) (Fig. 8) or diatom models, which may reflect differences in the predictive ability of the inference models (Fig. 9). Although chrysophyte cysts have been shown to be sensitive indicators of lake acidification (Smol 1995), cyst models generally do not perform as well as diatom or scaled chrysophyte models developed with comparable data sets. This may reflect variation associated with cyst taxonomy and identification. Furthermore, cysts represent a resting stage, and therefore abundances may not directly reflect conditions in the planktonic environment.

The existence of three models for inferring lakewater pH in the Muskoka region introduces an interesting dilemma for lake managers. On one hand, each model may provide unique ecological information that may be used to evaluate ecosystem-level changes in water quality. On the other hand, the lake manager is faced with three, different interpretations of change in the study lakes, and faces a difficult challenge of deciding which indicator to believe. One option is to take a conservative approach, and

base management decisions on the paleolimnological indicator that is inferring the greatest amount of change since pre-industrial times. However, this approach does not consider differences in the predictive ability of the individual inference models, and may also result in a loss of important ecological information. We propose an alternative approach which takes into account the predictive ability of each inference model, without sacrificing the ecological relationships of each indicator with its environment.

The combined reconstruction models, whether based on r^2-weighted mean or RMSE-weighted mean values, performed better than the models from individual indicators, when used to predict the measured pH of the modern samples (Fig. 9a and 9b). There are at least two reasons that may explain these trends. First, the combined models are calculated as averages of the indicator models, and therefore numerically smooth the biases associated with the individual models. For example, inference models from diatom and chrysophyte cysts under and overestimate the measured pH of samples with a pH < 6, respectively (Fig. 9a). Combining these inferences into a single prediction may have reduced the organism-specific biases, resulting in a inferred value close to the measured pH.

Second, when reconstructions from several indicators are combined, the biological record is smoothed, and may more appropriately match the resolution of the environmental data. In our training set, measured pH was calculated as an average of ice-free measurements over the 1990-1992 seasons. Similarly, the biological data of each indicator was smoothed temporally, representing the top 1-cm of each sediment core (approx. 2-5 years in this region). However, the deposition of each indicator is not

constant through the ice-free season. For example, several chrysophyte taxa reach population maxima immediately after ice-out, with smaller maxima in the fall (Sandgren 1988). The contribution of chrysophyte scales and cysts to the lake sediment may be dominated by seasonal periods of higher deposition. Therefore, combining the inferences of chrysophytes and diatoms may produce biological data that are more representative of the entire ice-free season, and reduce the impact of these seasonal biases. This is particularly important for environmental variables, such as pH, that vary during the ice-free season. Snow-melt in early spring may contribute acidic run-off to Ontario lakes, resulting in a significant decrease in pH at this time (Smol et al. 1998). This may also explain why chrysophyte models generally show a greater acidification trend than the diatom model in south-central Ontario (Hall and Smol, 1996; Wilkinson et al. 1999; this study), and in other regions (Davis et al. 1990; Cumming et al. 1992*b*; Dixit et al. 1992*a*; Sullivan et al. 1992).

The main disadvantage of combining inference models to infer lakewater pH is that the calculation of a mean reduces the impact of extreme values associated with each indicator, resulting in a smaller estimate of change since pre-industrial times. However, if the smoothed biological data are a more reliable fit with the environmental data, as suggested above, then the smaller inferred changes may reflect true changes in these lakes. It should be recognized that these models can only estimate environmental change at a resolution equal to that of the training set. Therefore, inferred changes in this study reflect mean conditions over two ice-free seasons. This combined inference approach may not be advantageous in other studies, where water chemistry data are representative

of single measures or seasonal values.

Multiple indicators in paleolimnological studies are useful in that they may provide information about environmental change at an ecosystem level. However, due to differences in the predictive power of individual reconstruction models, prediction and random errors, and differences in the ecological preferences of organisms, the magnitude and direction of inferred change may vary across indicators. From a lake management perspective, interpreting these differences may be difficult. We have explored the use of a single, mean inference from three phycological indicators, that is weighted by either the coefficient of determination of the reconstruction models, or the prediction error. This model performs as well or better than the individual models when used to predict the pH of modern samples. This suggests that the model is reliable, and can be used to infer the pH of lakes in south-central Ontario.

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Table 1. Latitude, longitude, and the measured pH of the 53 study lakes.

Lake code	Lake name	Latitude (N)	Longitude (W)	pH
1	12 Mile	45°01'	78°43'	7.0
2	Bass	45°07'	79°42'	6.3
3	Basshaunt	45°07'	78°28'	6.7
4	Bigwind	45°03'	78°04'	6.3
5	Blue Chalk	45°11'	78°56'	6.7
6	Boshkung	45°04'	78°44'	6.9
7	Bruce	45°11'	79°40'	6.8
8	Buck	45°22'	79°00'	6.5
9	Butterfly	45°05'	79°38'	7.0
10	Canning	44°57'	78°38'	7.3
11	Chub	45°13'	78°59'	5.7
12	Clear	45°11'	78°43'	5.8
13	Crosson	45°05'	78°02'	5.6
14	Dickie	45°09'	79°05'	5.9
15	Eagle	45°08'	78°29'	7.2
16	Frazer Island (L. Joseph)	45°15'	78°46'	6.7
17	Gravenhurst Bay (L. Muskoka)	44°56'	79°24'	7.2
18	Green	45°07'	78°37'	7.2
19	Gullfeather	45°06'	79°01'	5.8
20	Haliburton	45°13'	78°25'	7.0
21	Hall's	45°06'	78°44'	6.5
22	Hamer Bay (L. Joseph)	45°13'	79°46'	6.6
23	Hammel Bay (Three Mile L.)	45°10'	79°27'	7.2
24	Harp	45°23'	78°08'	6.4
25	Heney	45°08'	79°06'	5.8
26	Kashagawigamog North Basin	45°01'	78°34'	7.2
27	Kashagawigamog South Basin	45°01'	78°34'	7.2
28	Kelly	45°15'	78°37'	6.2
29	Kennisis	45°13'	78°39'	6.3
30	Kushog North Basin	45°08'	78°50'	6.5
31	Kushog South Basin	45°06'	78°48'	6.5
32	Leech	45°03'	79°06'	6.2
33	Leonard	45°04'	79°27'	6.0
34	Little Clear	45°24'	79°01'	6.9
35	Little Kennisis	45°15'	78°36'	6.1
36	Little Redstone	45°13'	78°34'	6.3
37	Maple	45°06'	78°40'	7.1
38	McKay	45°04'	78°10'	6.3
39	Moose	45°09'	78°28'	7.2
40	Muskoka Bay (L. Muskoka)	44°57'	79°24'	7.1
41	Oblong	45°11'	78°26'	7.1
42	Plastic	45°11'	78°50'	5.8
43	Red Chalk East Basin	45°11'	78°56'	6.5
44	Red Chalk Main Basin	45°11'	78°56'	6.3
45	Red Pine	45°12'	78°42'	6.3
46	Redstone	45°12'	78°32'	6.5
47	Roothog Island (Lake of Bays)	45°15'	79°00'	6.8
48	Seagull Rock (Lake of Bays)	45°15'	79°00'	6.7
49	Solitaire	45°24'	79°01'	6.7
50	Soyer's	45°01'	78°37'	7.0
51	St. Nora	45°09'	78°50'	6.3
52	Walker	45°24'	79°05'	6.7
53	Young	45°12'	79°33'	6.7

Table 2. Minimum, maximum, and mean values of 18 physical-chemical variables from the 53 study lakes.

Variable	Minimum	Maximum	Mean
pH	5.6	7.3	6.6
alkalinity ($mg.L^{-1}$ $CaCO_3$)	0.4	23.0	6.2
conductivity ($\mu S.cm^{-1}$)	22.2	87.0	43.3
DOC ($mg.L^{-1}$)	1.7	5.8	3.5
[Ca] ($mg.L^{-1}$)	1.8	14.2	4.3
[Mg] ($mg.L^{-1}$)	0.5	2.3	1.0
[Na] ($mg.L^{-1}$)	0.5	9.0	1.8
[K] ($mg.L^{-1}$)	0.2	1.00	0.6
[SO_4] ($mg.L^{-1}$)	4.2	9.4	7.5
[NH_3] ($\mu g.L^{-1}$)	5.0	83.9	20.2
[NO_3] ($mg.L^{-1}$)	2.0	247.0	103.6
[TN] ($mg.L^{-1}$)	140.0	380.0	236.2
[TP] spring overturn ($\mu g.L^{-1}$)	2.7	24.3	7.3
[Si] ($mg.L^{-1}$)	0.1	1.9	0.9
Surface area (ha)	10.9	1675.0	274.5
Watershed area (km^2)	127.6	89658.0	12388.5
Maximum depth (m)	5.8	82.4	31.9
$COT.SA^{-1}.Zmax$ ($\#.ha^{-1}.m$)[1]	0.0	1.3	0.6

[1] $COT.SA^{-1}.Zmax$ is an index of volume-weighted lakeshore development (Wilkinson et al. 1999).

Table 3. The number of occurrences, the effective number of occurrences (Hill's N2), mean, and maximum relative abundances of the 24 taxa that occurred in at least three lakes, and had a relative abundance of >1% in at least one of the 53 study lakes.

Taxon code	Taxon	number of occurrences	N2	mean	max
A	*Mallomonas acaroides v. muskokana*[1] Nicholls	21	9.35	0.71	7.13
B	*M. akrokomas* Ruttner in Pascher	34	22.66	0.52	2.34
C	*M. allorgei* (Defl.) Conrad	9	3.39	0.16	4.18
D	*M. caudata* Ivanov *em.* Krieger	53	30.22	4.01	19.56
E	*M. crassiaquama* (Asmund) Fott	53	37.21	8.93	24.26
F	*M. duerrschmidtiae* Siver, Hamer & Kling	52	17.20	6.54	43.24
G	*M. elongata* Reverdin	36	23.53	0.57	3.17
H	*M. hamata* Asmund	50	28.87	3.83	14.50
I	*M. heterospina* Lund	20	9.96	0.24	2.49
J	*M.* 'medium' group[2]	35	16.80	0.55	3.43
K	*M. pseudocoronata* Prescott	52	15.40	3.34	34.24
L	*M. punctifera* Korsh.	27	16.88	0.44	2.74
M	*M.* 'small' group[3]	47	29.34	0.93	3.44
N	*M. tonsurata* Teiling *em.* Krieger	46	23.51	1.09	6.34
O	*M. torquata* Asmund and Cronberg	49	29.76	0.67	2.97
P	*Synura curtispina* (Petersen & Han.) Asmund	40	14.04	1.82	13.79
Q	*S. echinulata* Korsh.	52	18.13	8.45	50.87
R	*S. petersenii* Korsh.	53	36.78	28.13	72.24
S	*S. sphagnicola* Korsh.	47	20.14	13.99	67.66
T	*S. spinosa* Korsh.	52	28.50	4.56	17.98
U	*S. uvella* Stein em. Korsh.	45	17.64	4.33	32.84
V	*Chrysosphaerella* Lauterborn[4]	52	19.12	4.95	36.03
W	*Paraphysomonas* deSaedeleer	32	22.48	0.33	1.69
X	*Spiniferomonas* Takahashi	49	32.93	0.67	2.74

[1] may include the nominate variety in some samples
[2] includes unidentified *Mallomonas* scales larger than *M.* 'small', e.g. *M. intermedia* Kisselew and *M. corymbosa* Asmund & Hillard
[3] includes small unidentified *Mallomonas* scales, e.g. *M. galeiformis* Nicholls
[4] includes *C. brevispina* Korshikov and *C. longispina* Lauterborn *em.* Nicholls

Table 4. Canonical coefficients, approximate *t*-test values, and intraset correlations of the environmental variables for each of the first three RDA axes.

	Canonical coefficients			t values			Intraset correlations		
Variable	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
pH	-1.10	-0.14	0.27	-12.69*	-0.92	0.95	-0.80	-0.15	-0.19
DOC	0.08	-0.74	-0.06	1.12	-5.94*	-0.26	0.09	-0.72	-0.03
log[Na]	0.47	-0.15	-0.63	5.31*	-0.99	-2.11*	-0.16	-0.27	-0.31
$[SO_4]$	-0.11	-0.44	-0.25	-1.24	-2.91*	-0.85	-0.50	-0.07	-0.14
$\log[NH_3]$	-0.21	-0.14	0.93	-2.86*	-1.11	3.76*	0.18	-0.30	0.48
$[NO_3]$	-0.20	0.56	0.36	-2.07*	3.45*	1.13	-0.47	0.25	-0.17

* significant at $p \leq 0.05$

List of Figures

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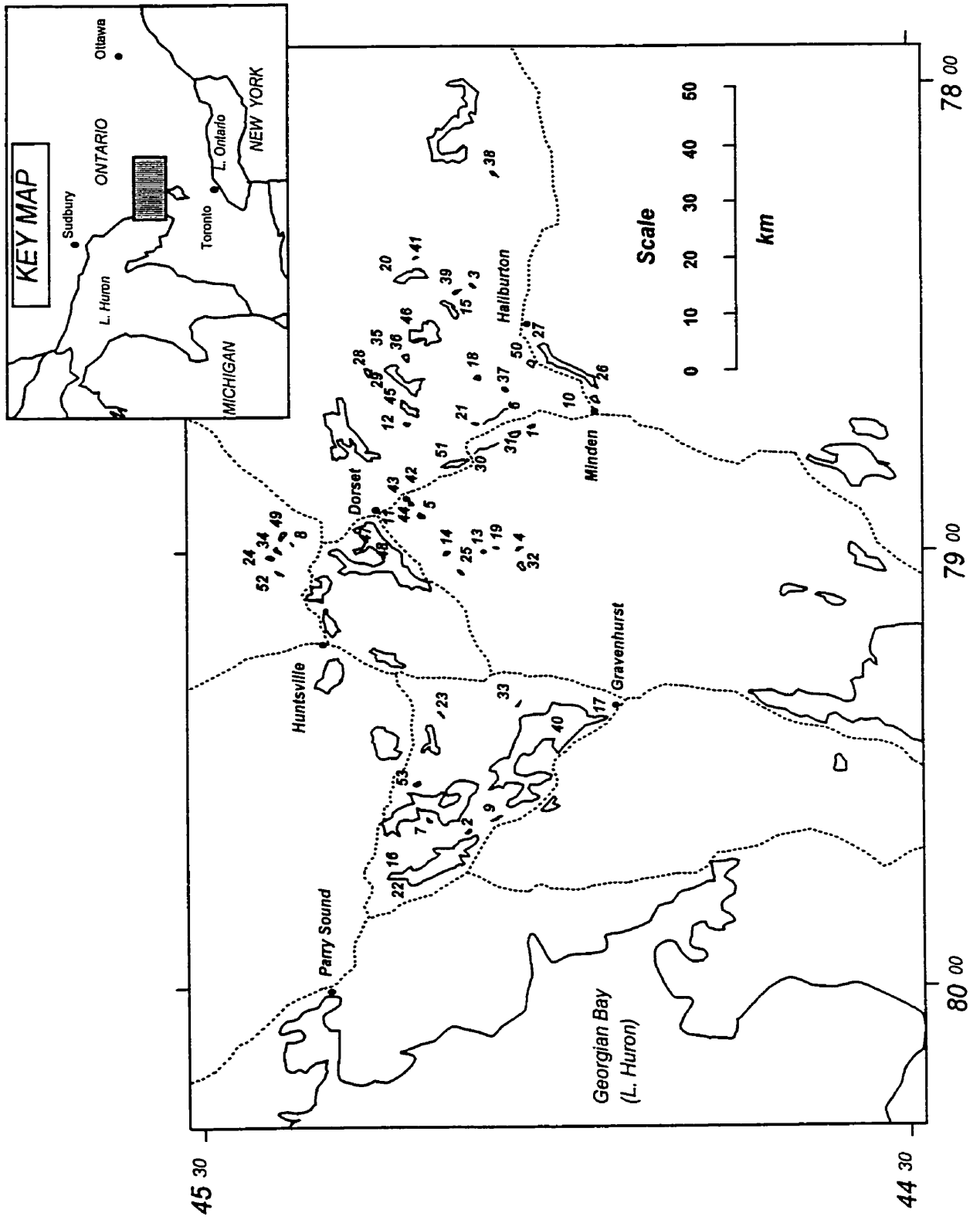

KEY MAP
Sudbury
Ottawa
ONTARIO
L. Huron
Toronto
L. Ontario
NEW YORK
MICHIGAN
Scale
0 10 20 30 40 50
km
Dorset
Minden
Haliburton
Huntsville
Gravenhurst
Parry Sound
Georgian Bay
(L. Huron)
45 30
44 30
80 00
79 00
78 00

Figure 1

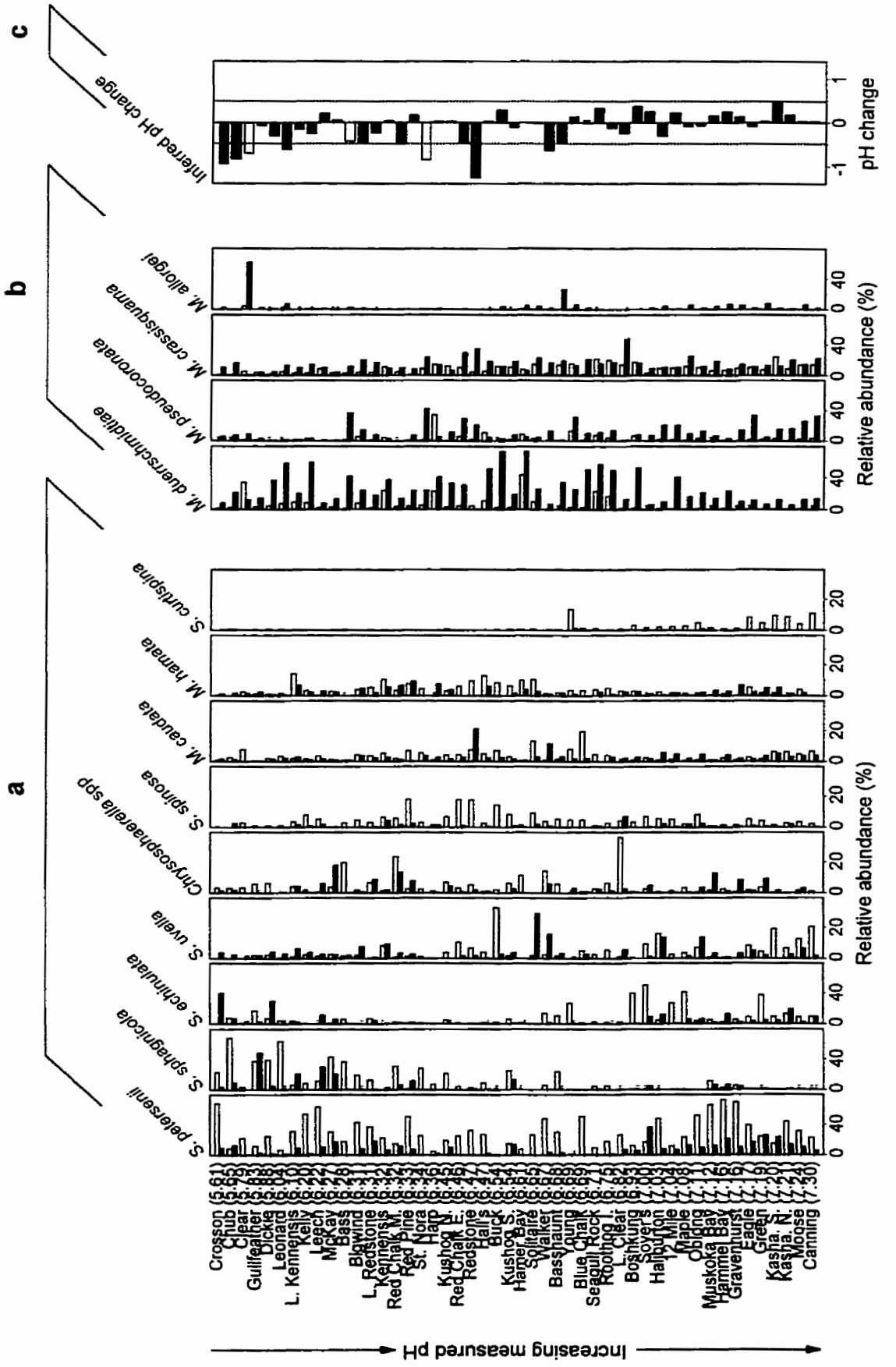

a
b
c
S. peiersenii
S. sphagnicola
S. echinulata
S. uvella
Chrysosphaerella spp
S. spinosa
M. caudata
M. hamata
S. curtispina
M. duerrschmidtiae
M. pseudocoronata
M. crassisquama
M. allorgei
Relative abundance (%)
Inferred pH change
pH change
Increasing measured pH
Crosson (5.61)
Chub (5.66)
Clear (5.83)
Gullfeather (5.88)
Dicks (6.04)
Leonard (6.10)
L. Kennensis (6.20)
Kelly (6.22)
Leech (6.27)
McKay (6.27)
Bass (6.28)
Blagwind (6.31)
L. Redstone (6.32)
Kennensis (6.32)
Red Chalk M. (6.32)
Red Pine (6.42)
St. Nora (6.44)
Harp (6.46)
Kushog N. (6.46)
Red Chalk E. (6.47)
Redstone (6.47)
Hall's (6.54)
Buck (6.54)
Kushog S. (6.57)
Harmer Bay (6.61)
Solitaire (6.67)
Walker (6.68)
Basshaunt (6.69)
Young (6.69)
Blue Chalk (6.71)
Seagull Rock (6.82)
Rootlong (6.85)
L. Clear (6.93)
Boshkung (6.93)
Sovers (7.03)
Halfway (7.03)
1 Mile (7.08)
Maple (7.12)
Oblong (7.12)
Muskoka Bay (7.16)
Hammel Bay (7.16)
Gravenhurst (7.19)
Eagle (7.19)
Green (7.19)
Kasha. S. (7.20)
Kasha. N. (7.21)
Moose (7.24)
Canning (7.30)

Figure 2

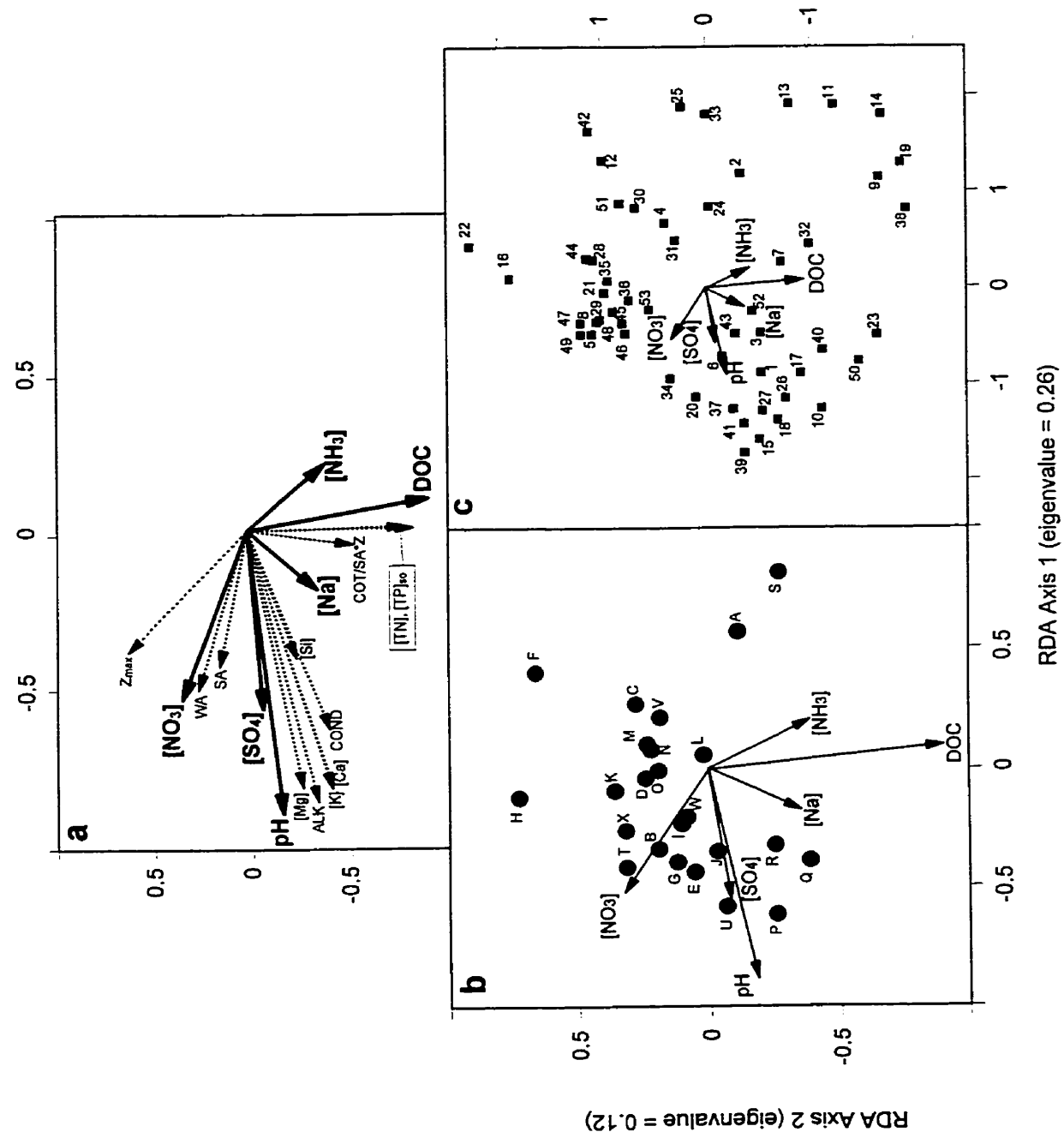

a
b
c
[NO3]
[SO4]
pH
[NH3]
DOC
[Na]
[Si]
[Mg]
[K]
[Ca]
ALK
COND
WA
SA
Zmax
COT/SA*Z
RDA Axis 1 (eigenvalue = 0.26)
RDA Axis 2 (eigenvalue = 0.12)

Figure 3

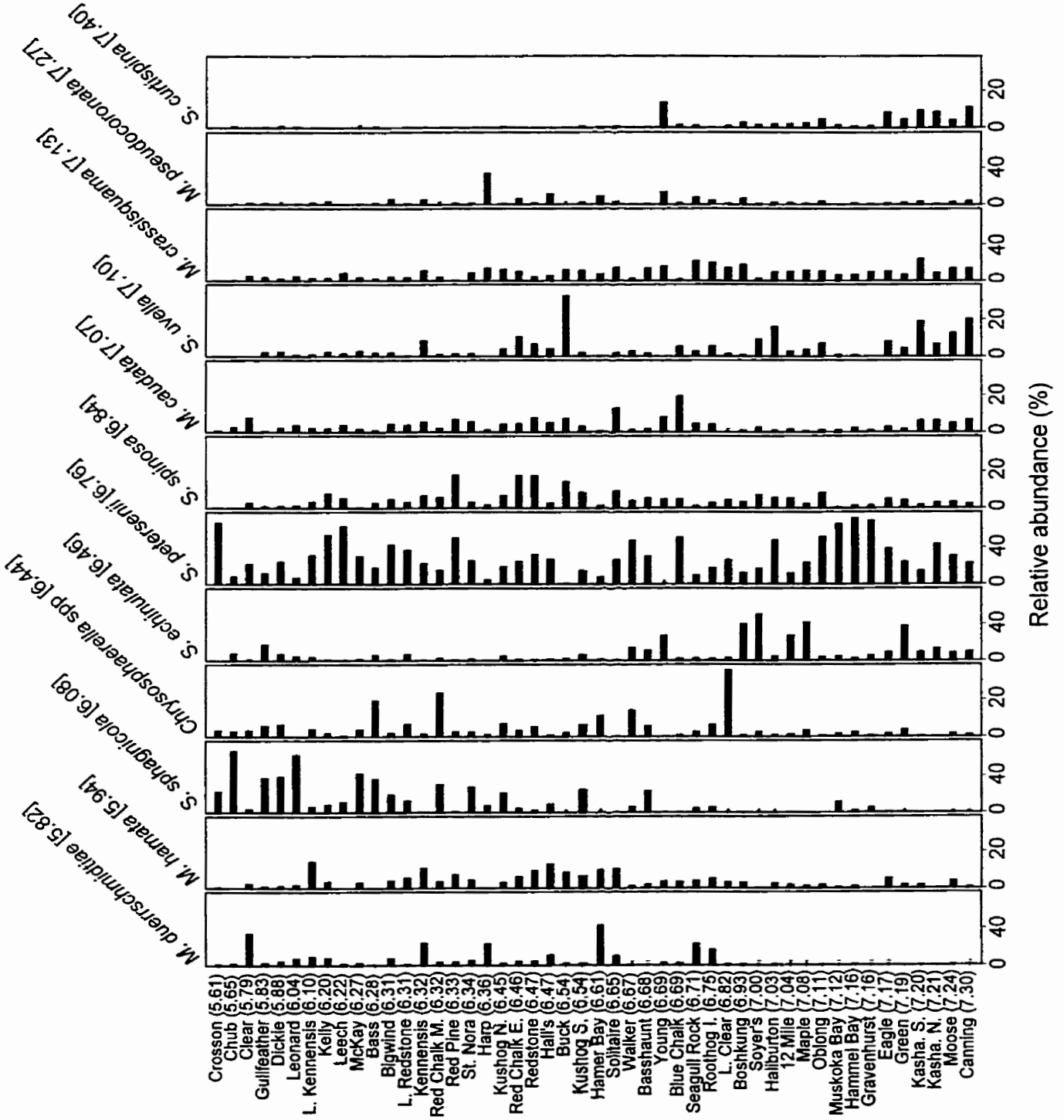
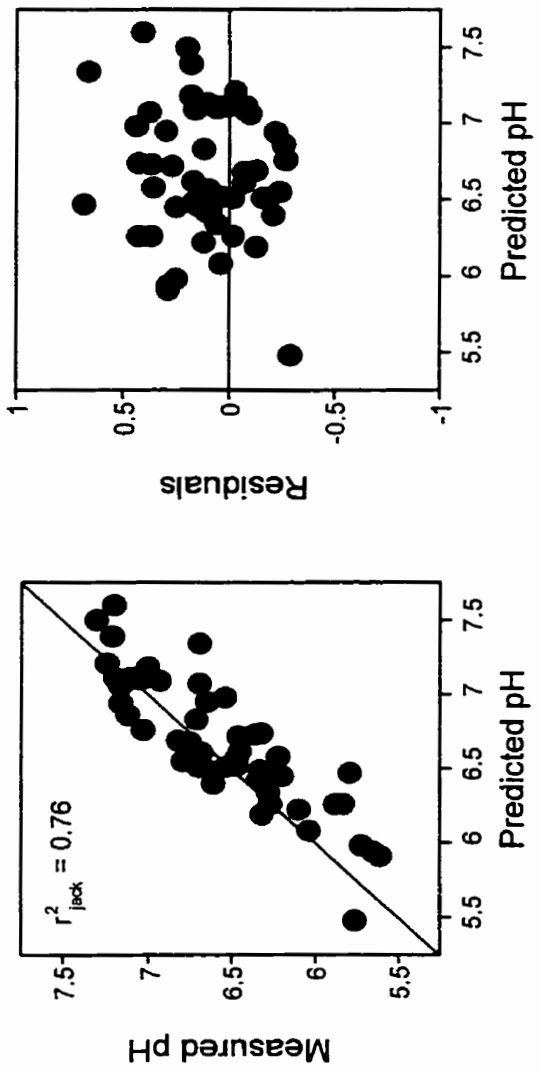

M. duerschmidtiae [5.82]
M. hamata [5.94]
S. sphagnicola [6.08]
Chrysosphaerella spp [6.44]
S. echinulata [6.46]
S. peterseni [6.76]
S. spinosa [6.84]
M. caudata [7.07]
S. uvella [7.10]
M. crassisquama [7.13]
M. pseudocoronata [7.27]
S. curtispina [7.40]
Relative abundance (%)
0 40 0 20 0 40 0 40 0 20 0 20 0 20 0 40 0 40 0 20 0 40 0 20
Crosson (5.61)
Chub (5.65)
Clear (5.79)
Gullfeather (5.83)
Dickie (5.88)
Leonard (6.04)
L. Kennensis (6.10)
Kelly (6.20)
Leech (6.22)
McKay (6.27)
Bass (6.28)
Bigwind (6.31)
L. Redstone (6.31)
Kennensis (6.32)
Red Chalk M. (6.32)
Red Pine (6.33)
St. Nora (6.34)
Harp (6.36)
Kushog N. (6.45)
Red Chalk E. (6.46)
Redstone (6.47)
Hall's (6.47)
Buck (6.54)
Kushog S. (6.54)
Hamer Bay (6.61)
Soiltaire (6.65)
Walker (6.67)
Basshaunt (6.68)
Young (6.69)
Blue Chalk (6.69)
Seagull Rock (6.71)
Roothog I. (6.75)
L. Clear (6.82)
Boshkung (6.93)
Soyers (7.00)
Haliburton (7.03)
12 Mile (7.04)
Maple (7.08)
Oblong (7.11)
Muskoka Bay (7.12)
Hammel Bay (7.16)
Gravenhurst (7.16)
Eagle (7.17)
Green (7.19)
Kasha. S. (7.20)
Kasha. N. (7.21)
Moose (7.24)
Canning (7.30)

Figure 4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0.5
0
-0.5
-1
5.5
6
6.5
7
7.5
Predicted pH
Measured pH
7.5
7
6.5
6
5.5
r^2_{jack} = 0.76
5.5
6
6.5
7
7.5
Predicted pH

Figure 5

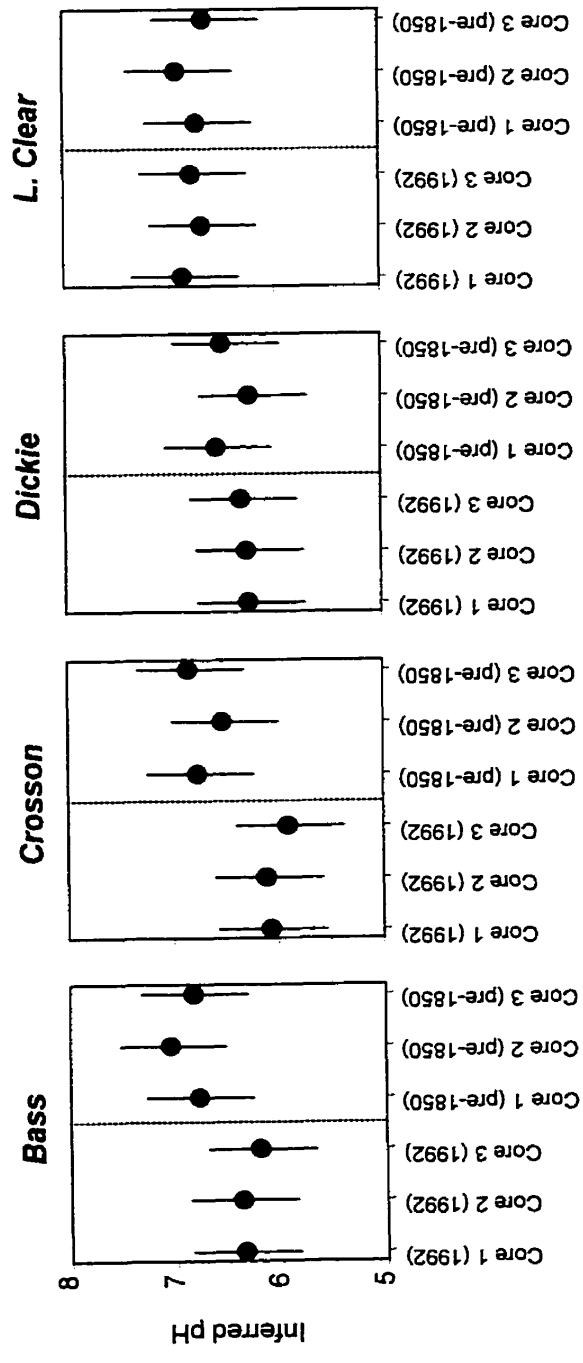
Bass
Crosson
Dickie
L. Clear
Core 1 (1992)
Core 2 (1992)
Core 3 (1992)
Core 1 (pre-1850)
Core 2 (pre-1850)
Core 3 (pre-1850)
8
7
6
5
Inferred pH

Figure 6

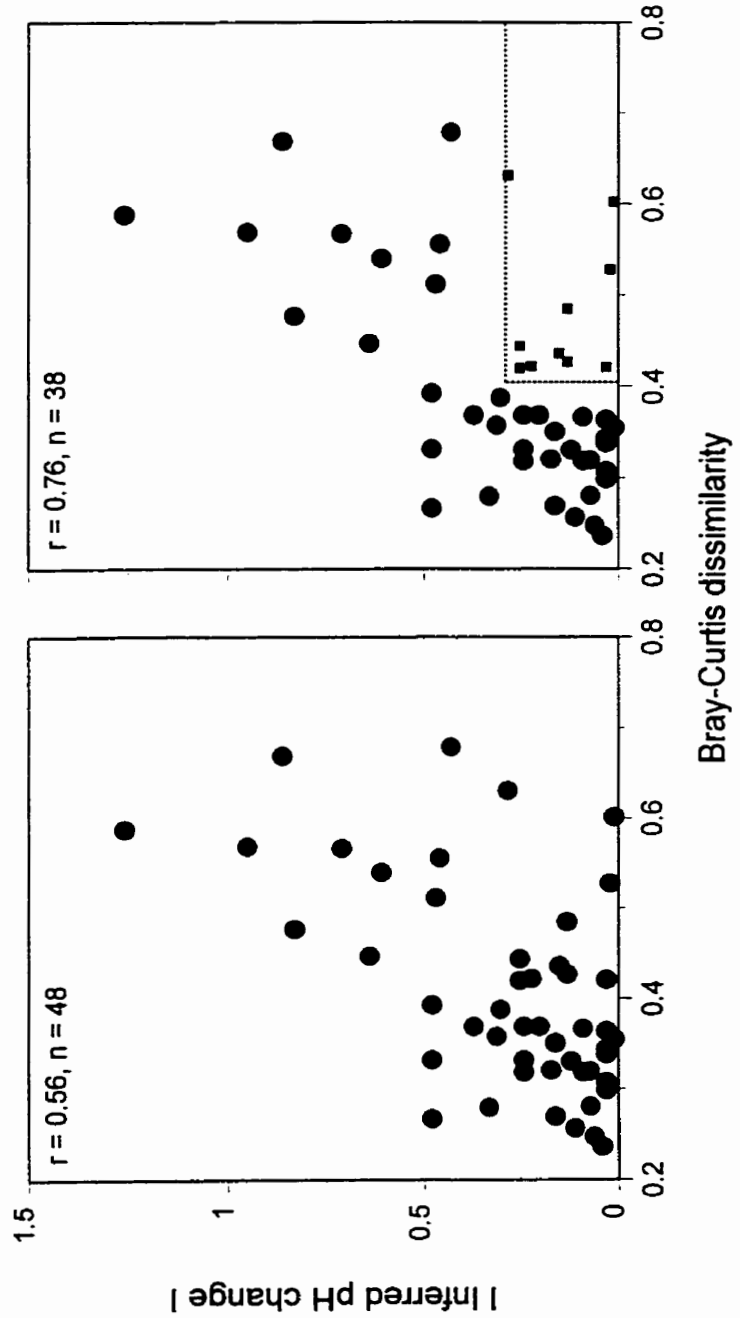
r = 0.56, n = 48
r = 0.76, n = 38
| Inferred pH change |
Bray-Curtis dissimilarity
0
0.5
1
1.5
0.2
0.4
0.6
0.8

Figure 7

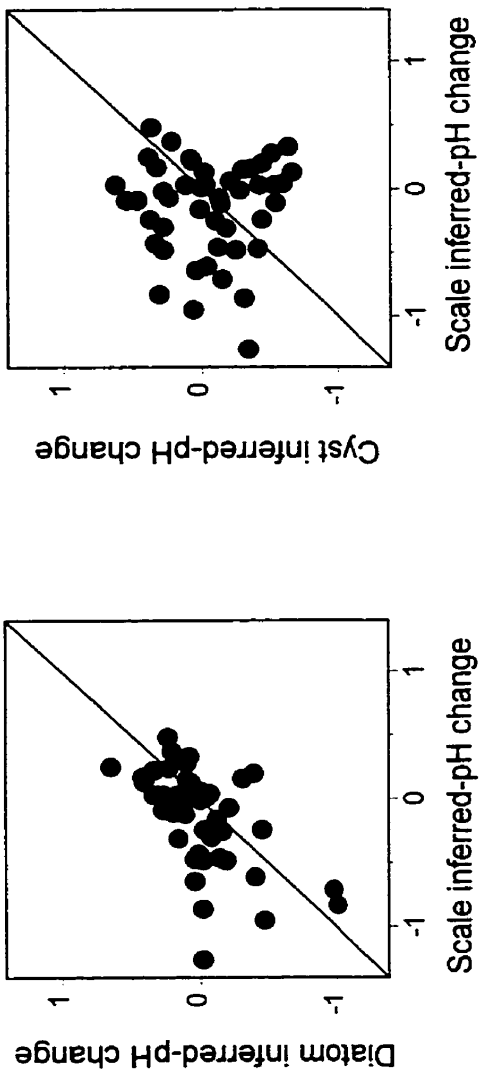
Cyst inferred-pH change
1
0
-1
-1
0
1
Scale inferred-pH change
Diatom inferred-pH change
1
0
-1
-1
0
1
Scale inferred-pH change

Figure 8

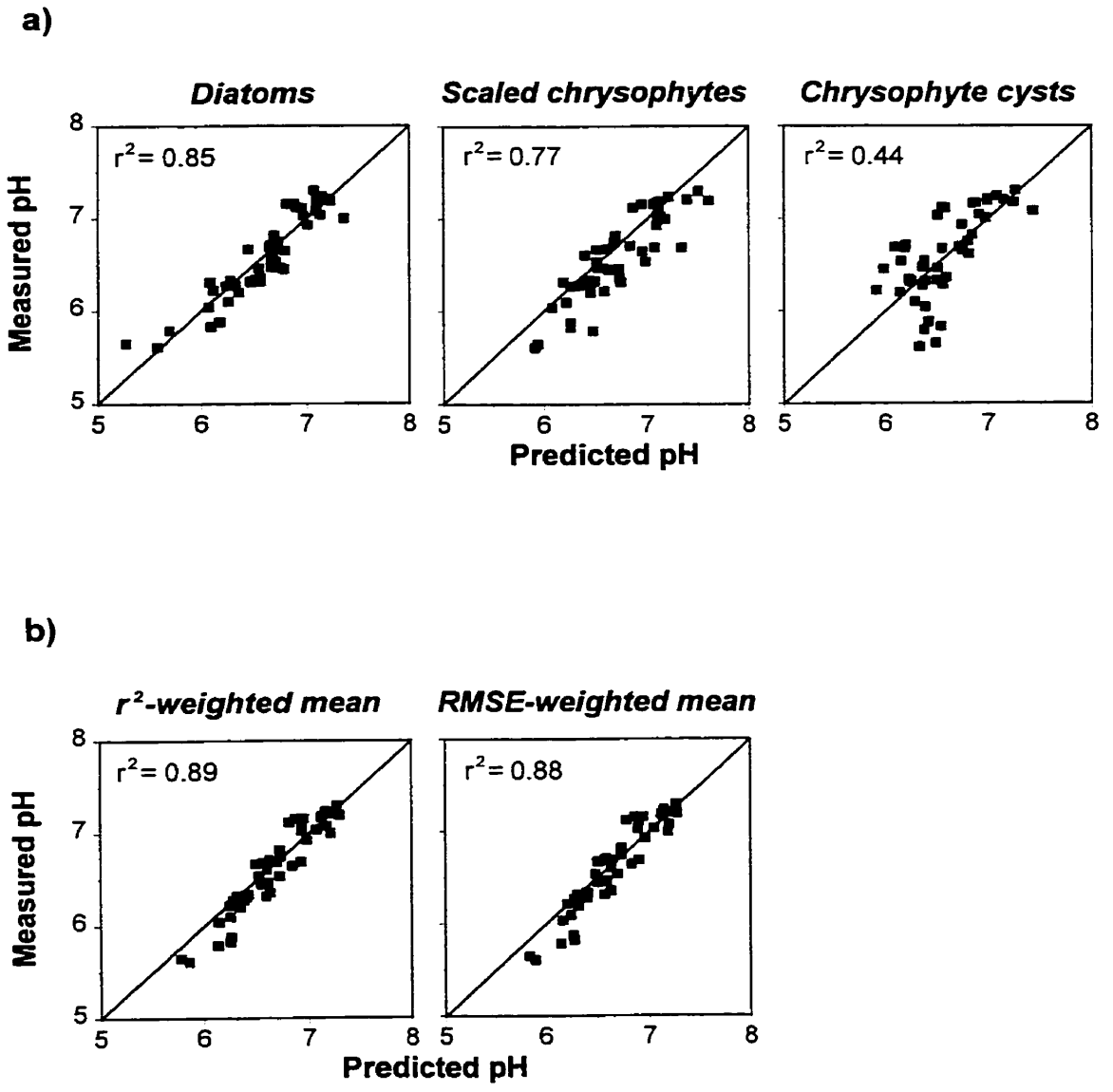
a)
Diatoms
Scaled chrysophytes
Chrysophyte cysts
r²= 0.85
r²= 0.77
r²= 0.44
Measured pH
Predicted pH
b)
r²-weighted mean
RMSE-weighted mean
r²= 0.89
r²= 0.88
Measured pH
Predicted pH

Figure 9

CHAPTER 5

REGIONAL INCREASES IN TASTE AND ODOUR-CAUSING CHRYSOPHYTES IN CANADIAN SHIELD LAKES

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Key words: Taste and odour, scaled chrysophytes, *Synura petersenii*, Canadian Shield lakes

Abstract

As measured by a rise in the number of complaints by local users, taste and odour events have increased over the past twenty years in Ontario Shield lakes. Chrysophytes have been shown to be the causative organisms. Specifically, blooms associated with the scaled chrysophyte, *Synura petersenii*, have been widespread. Using paleolimnological techniques, we tracked changes in the relative abundance of *S. petersenii* in 48 Shield lakes in south-central Ontario since pre-industrial times. An examination of scaled chrysophytes in top (present-day) and bottom (pre-industrial) sediment samples determined that *S. petersenii* was the most dominant taxon in the modern sediment samples, and has increased in relative abundance in nearly all of lakes. This trend suggests that the threat of taste and odour events has increased in south-central Ontario lakes, and that one or more regional, anthropogenic stressors is involved. However, canonical variates analysis found no significant relationship between *S. petersenii* abundances and acidification or eutrophication-related variables. We discuss the importance of other factors, including long-term changes in lake water transparency, as possible explanations for the observed trends.

Introduction

Lakewater pH has been shown to be an important variable influencing the distribution of scaled chrysophyte taxa in south-central Ontario lakes (Chapter 3). However, in some lakes, there exist species changes that are not related to inferred changes in lakewater pH. The scaled chrysophyte *Synura petersenii* is one species that has increased in relative abundance in many lakes, irrespective of changes in lakewater pH (Chapter 4)

The past twenty years has seen a rise in the number of user complaints associated with algal blooms in south-central Ontario lakes (Nicholls, 1995, and personal communication). While chrysophytes of the genus *Uroglena* have been implicated as the causative organisms in some of these lakes, taste and odour events caused by the scaled chrysophyte *S. petersenii* appear to be more widespread (Nicholls & Gerrath, 1985; Nicholls, 1995). A visible colouration of the water, and a "fishy" or "cucumber" odour, are the most common complaints that have been received (Nicholls, 1995). A recent compilation suggests that these events are occurring in a variety of lakes, spanning a range of environmental conditions (Nicholls & Gerrath, 1985; K.H. Nicholls, Ontario Ministry of the Environment, personal communication). However, these reports are based solely on complaints from the general public, and there is presently no scientific knowledge of long-term trends in taste and odour blooms in Canadian Shield lakes.

S. petersenii is a large, colonial, scaled chrysophyte that often forms metalimnetic populations during periods of stable stratification (Sandgren, 1988). Considered a generalist with respect to many environmental variables (Siver, 1995), it has been reported to be the most abundant taxon in a number of chrysophyte surveys (e.g.

Connecticut: Siver, 1987; Iowa: Wee, 1982, and Minnesota: Wujek et al., 1981). *S. petersenii* has been found to prefer cold water habitats (i.e., during the cold months, or in colder waters below the thermocline), reaching maximum abundances in waters below 12°C (Siver, 1987, and references therein). *S. petersenii* produces siliceous scales that can be used to track its abundance relative to other scaled chrysophyte taxa (Smol, 1995). In other studies, paleolimnological records suggest that this species is generally more common in recent sediment samples (i.e., last ~ 75 years) than in pre-industrial times, and often increases in abundance beginning in the early to mid-1900s (e.g. Dixit et al., 1992). Several, at times contradictory, hypotheses have been suggested to explain the increase in *S. petersenii* in many North American lakes, including land-use (Marsicano & Siver, 1993, Dixit et al., 1992), nutrient enrichment (Lott et al., 1994), and atmospheric deposition (Nicholls & Gerrath, 1985; Kodama et al., 1997). These findings suggest that the environmental conditions that are most suitable for the growth of *S. petersenii* are not well understood.

Presently, our understanding of taste and odour events has relied solely on complaints from local users. However, these are often biased, as they may exclude remote lakes, and are often restricted to the summer, recreational season. Furthermore, some events may not be reported in this region, as many local users do not rely on lake water for drinking purposes (Nicholls, 1995). Therefore, two main questions remain unanswered with respect to taste and odour events in south-central Ontario lakes. First, is the threat of taste and odour events, as caused by *S. petersenii,* regional in south-central Ontario lakes (Nicholls & Gerrath, 1985)? Second, has this threat increased since pre-

industrial times as a result of anthropogenic disturbances, or have problems always been common? In this study, we use paleolimnological techniques to provide evidence that *S. petersenii* is presently the most abundant taxon in many lakes in south-central Ontario. Second, we show that the regional abundance of *S. petersenii* has increased dramatically since pre-industrial times. These results strongly suggest that taste and odour events are increasing in south-central Ontario lakes, and that direct or indirect human activities may be responsible.

Methods

The Muskoka-Haliburton region of south-central Ontario is underlain by Precambrian granitic bedrock of the Canadian Shield (Jeffries & Snyder, 1983). A marble intrusion, found in the eastern portion of the study area, encompasses twelve of the study lakes. Soils are generally shallow and acidic, although thicker deposits of clay, sand, or gravel occur locally (Chapman & Putnam, 1984). Much of this region is characterized by secondary mixed-deciduous and coniferous forests, following widespread deforestation in the mid to late-1800s (Michalski et al., 1973). Agriculture is minimal in the region, due to the rough topography, thin soils, and cool climate. Presently, human activity consists primarily of recreational activities associated with seasonal cottages and rural municipalities.

In the fall of 1992, sediment cores were removed from the deepest basin of 48 lakes in the Muskoka-Haliburton region of south-central Ontario (Hall & Smol, 1996). The cores were sectioned at the lakeshore into stratigraphic sections using a Glew (1988)

vertical extruder. Two sediment sections were examined: the top centimetre (present-day lake conditions), and a 1-cm interval taken at a minimum core depth of 20-cm (pre-industrial lake conditions). Although the precise date of the bottom sample of each core is not known, radiometric ^{210}Pb-dating of other cores from the south-central Ontario region has shown that background conditions (> 120 years) are typically reached at core depths of 15-20 cm (e.g. Clerk et al., 2000; Dixit et al., 1990; Dixit et al., 1992). Water chemistry data were collected from 1990 to 1992 by personnel of the Ontario Ministry of the Environment, and are summarized in Hall & Smol (1996). A minimum of 300 chrysophyte scales were identified and enumerated along transects, using oil immersion at a magnification of 1500X (Chapter 4).

Canonical variates analysis was used to determine if linear combinations of physical-chemical environmental variables could discriminate lakes dominated by *Synura petersenii*, from lakes dominated by other species (i.e., *S. echinulata, S. sphagnicola, Mallomonas* taxa). CVA with a forward selection step was performed using CANOCO version 4 (ter Braak & Šmilauer, 1998).

Results

Thirty-two scaled chrysophyte taxa or groups were identified in the present-day sediment samples of the study lakes. The most abundant chrysophyte taxon in the modern samples was *Synura petersenii*, reaching relative abundances of greater than 30% in 20 of the lakes (Fig. 1a). However, pre-industrial abundances of *S. petersenii* were much lower, present at a mean relative abundance of 8% (Fig. 2). *S. sphagnicola* and *S. echinulata*

also contributed to the high total *Synura* abundances, with average relative abundances of 14% and 8%, respectively (Fig. 1a). By comparison, the most abundant *Mallomonas* taxa in the surface samples were *M. crassisquama* and *M. duerrschmidtiae*, with average relative abundances of 9% and 7%, respectively. In contrast, *M. duerrschmidtiae* and *M. crassisquama* were the most abundant taxa in the pre-industrial time period, occurring at mean relative abundances of 26% and 15% across all lakes (Fig. 1b).

Canonical variates analysis (CVA), with forward selection, identified three environmental variables that could significantly differentiate between the groups (see Methods). The first and second CVA axes (Fig. 3a) captured gradients of pH-related variables, and DOC and nutrients, respectively. Clusters of lakes dominated by *S. echinulata*, *S. sphagnicola*, and *Mallomonas* species were separated along the first CVA axis, supporting previous studies showing that pH is an important variable influencing the distribution of chrysophyte taxa (Cumming et al., 1992; Chapter 3) (Fig. 3b). However, lakes dominated by *S. petersenii* could not be differentiated from other groups along the first or second CVA axes (Fig. 3c).

Discussion

Over the past twenty years, casual reports of taste and odour (T&O) events have increased steadily in the Muskoka-Haliburton region (Nicholls, 1995). It was not known, however, if this was caused by a real increase in problem algae, or simply an increased awareness of the problem. Our paleolimnological data suggest that the number of lakes that are susceptible to T&O chrysophyte blooms may be considerably greater than have

been reported by local users. *Synura petersenii*, which has been identified as the only scaled chrysophyte linked to T&O events in Ontario (Nicholls & Gerath, 1985), presently dominates the species assemblage of approximately half of the study lakes (Fig. 1a). Furthermore, recent evidence suggests that there may be a link between high *S. petersenii* abundances and the occurrence of T&O events. For example, this taxon dominated the modern sample of Solitaire Lake (i.e. 1990-1992) (Chapter 4), which was reported to have a T&O bloom in 1994 (Ken Nicholls, Ontario Ministry of the Environment, pers. comm.), approximately two years after the lake was sampled for this study.

A comparison of modern and fossil sediment intervals indicates that there has been a regional shift in the floristic composition of scaled chrysophytes, from an assemblage dominated by *Mallomonas* to one dominated by *Synura* species. The taxon *S. petersenii* showed the greatest mean change since pre-industrial times, and increased in relative abundance in greater than 90% of the study lakes. In other paleolimnological studies, large increases in *S. petersenii* were detected predominantly in circumneutral lakes receiving acidic deposition that have shown little change in lakewater pH since pre-industrial times (e.g. Sudbury region: Dixit et al., 1990; Connecticut: Marsicano & Siver, 1993; Adirondack Park: Cumming et al., 1994). Several hypothesis, including land-use (Dixit et al., 1992; Marsicano & Siver, 1993) and nutrient enrichment (Lott et al., 1994), have been proposed to explain these trends in other lakes. However, in our study there were no trends between these variables and increases in *S. petersenii*, with increases occurring in: 1) acidic and more alkaline lakes; 2) oligotrophic and mesotrophic lakes; and 3) lakes with and without watershed development (e.g. cottages or resorts).

A long-term change in water transparency is an alternative hypothesis that may explain the observed trends in chrysophyte assemblages. Recent warm temperatures, unusually strong El Niño events in the 1980s and early 1990s (Dillon et al., 1997), the long-term effects of acid precipitation (Dillon et al., 1987), and the interactive effects of these variables on lakewater transparency (Schindler et al., 1996), may have contributed to the observed species trends in this study. Colonial (e.g. *Synura*), and large unicellular chrysophytes (e.g. *Mallomonas caudata*) have increased in abundance in many lakes, and may selectively form deep-water peaks below the thermocline (Sandgren, 1988). Large chrysophytes are often most successful in clear lakes when the photic zone extends beyond the thermocline, a pattern that was detected at the Experimental Lakes Area during a twenty-year drought (Schindler et al., 1990). Furthermore, changes in water transparency may increase the zone of subthermocline production (Schindler et al., 1996), increasing the habitat of metalimnetic chrysophytes (Sandgren, 1988). Finally, deep-water populations may also have an advantage over epilimnetic taxa, as they may be protected from increased UV-B radiation associated with increased water transparency (Leavitt, et al., 1999; Xenopoulos et al., 2000). Long-term trends in dissolved organic carbon concentrations are presently being examined in Ontario Shield lakes, and may provide additional support for this hypothesis.

The importance of top-down controls on chrysophyte populations is poorly understood (Sandgren, 1988). Sandgren & Walton (1995) suggest that increased size and motility are two advantages that large, colonial chrysophytes may have over smaller forms when predation from small zooplankton taxa is high. However, this advantage

does not exist when the zooplankton assemblage is dominated by large *Daphnia* taxa (Sandgren & Walton, 1995). It is possible that the gradual decline of large piscovores, from decades of recreational fishing, may have altered the trophic structure of the lake, resulting in an increase in planktivorous fish taxa. Ultimately, this may have led to subsequent increases in smaller zooplankton forms and larger, colonial chrysophytes. Unfortunately, neither long-term fisheries data nor information on zooplankton size structure is available for these lakes. However, many cladoceran taxa leave remains in the sediment record which may be used in the future to obtain long-term changes of size structure.

In conclusion, we recognize that T&O chrysophyte blooms are triggered by a combination of factors that are presently not well understood (Nicholls, 1995), and that high abundances of *S. petersenii* may exist without producing T&O episodes (P.A. Siver, Connecticut College, personal communication). Furthermore, we acknowledge that the sediment record cannot be used to detect individual bloom events, which may last for less than two weeks in some lakes. Despite these limitations, our results clearly indicate that the threat of T&O events exists in many circumneutral lakes in south-central Ontario, and this threat has greatly increased since pre-industrial times. Therefore, it is likely that the observed species trends are the result of one or more regional, anthropogenic stressors on lake environments.

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List of figures

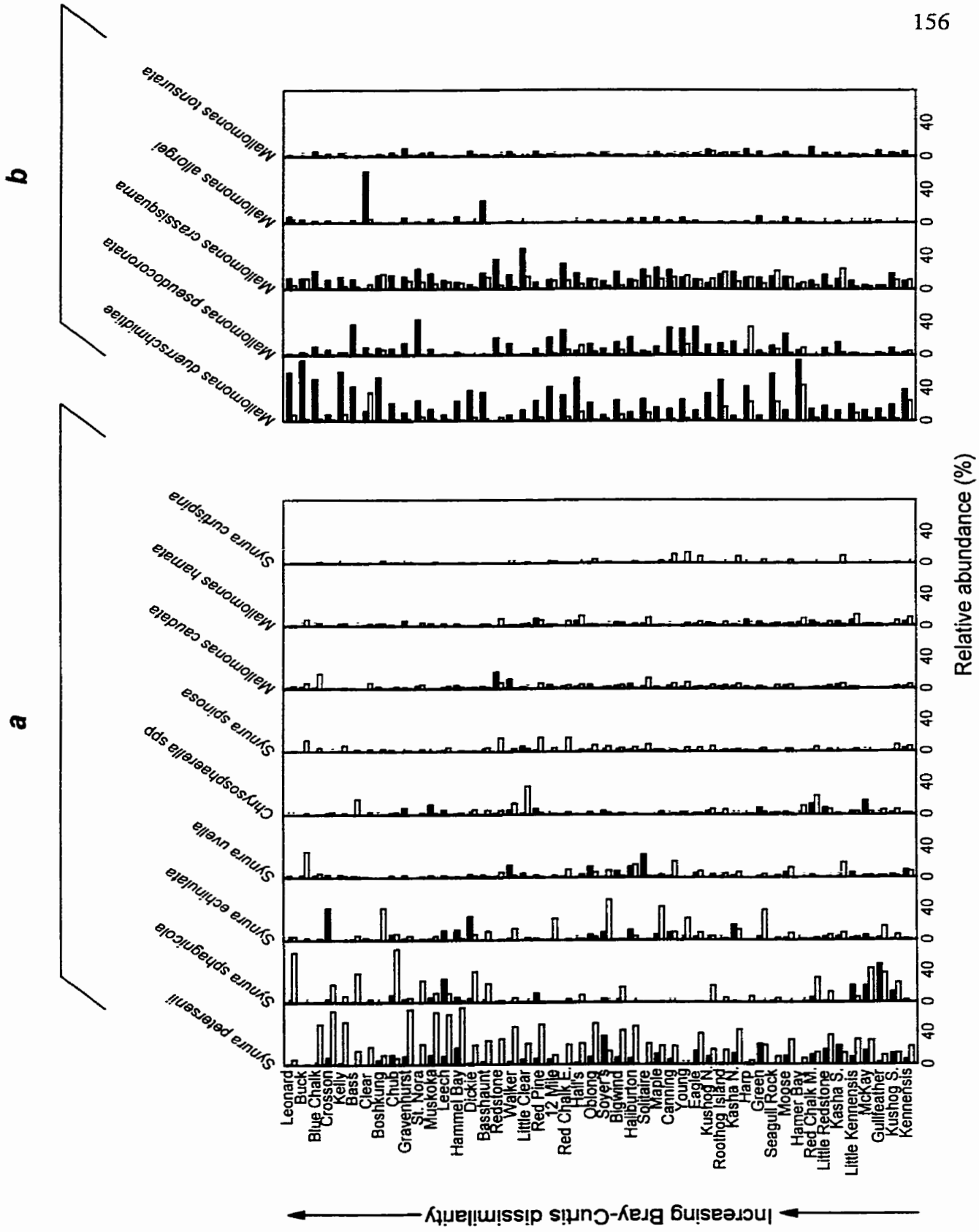

a
b
Synura petersenii
Synura sphagnicola
Synura echinulata
Synura uvella
Chrysosphaerella spp
Synura spinosa
Mallomonas caudata
Mallomonas hamata
Synura curtispina
Mallomonas duerschmidtiae
Mallomonas pseudocoronata
Mallomonas crassisquama
Mallomonas allorgei
Mallomonas lonsurata
0 40
Leonard
Buck
Blue Chalk
Crosson
Kelly
Bass
Clear
Boshkung
Chub
Gravenhurst
St. Nora
Muskoka
Leech
Hammel Bay
Dickie
Basshaunt
Redstone
Walker
Little Clear
Red Pine
12 Mile
Red Chalk E.
Hall's
Oblong
Soyers
Bigwind
Haliburton
Solitaire
Maple
Canning
Young
Eagle
Kushog N.
Roothog Island
Kasha N.
Harp
Green
Seagull Rock
Moose
Hamer Bay
Red Chalk M.
Little Redstone
Kasha S.
Little Kennensis
McKay
Guilleather
Kushog S.
Kennensis
Increasing Bray-Curtis dissimilarity
Relative abundance (%)

Figure 1

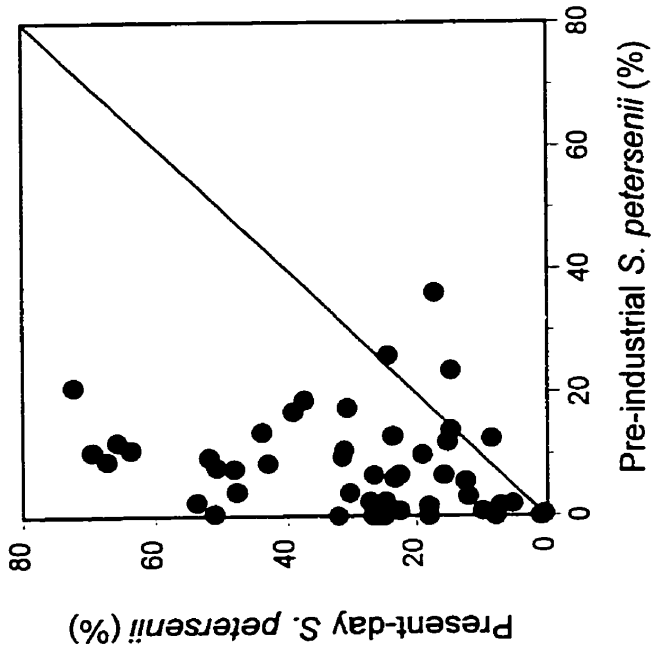
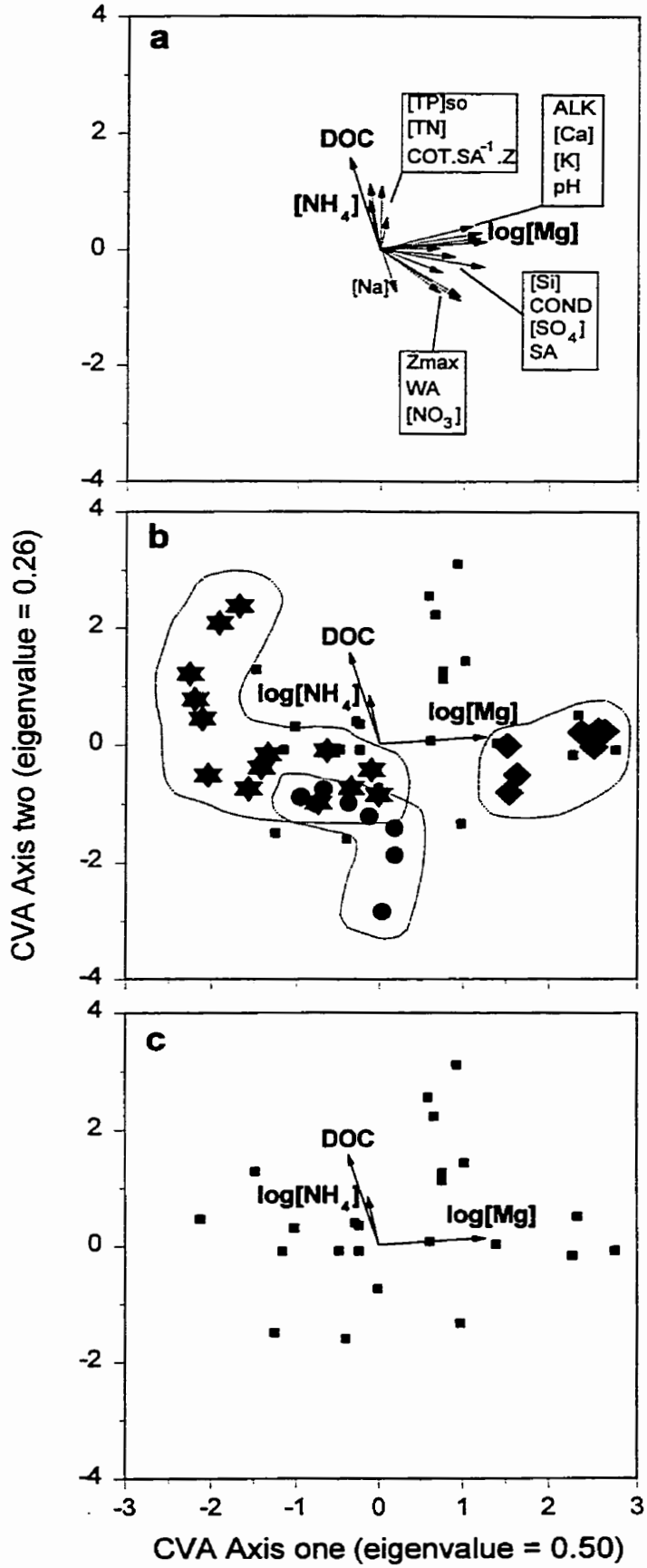

Pre-industrial S. petersenii (%)
Present-day S. petersenii (%)
0
20
40
60
80

Figure 2


a
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ALK
[Ca]
[K]
pH
DOC
[NH4]
log[Mg]
[Na]
[Si]
COND
[SO4]
SA
Zmax
WA
[NO3]
b
DOC
log[NH4]
log[Mg]
c
DOC
log[NH4]
log[Mg]
CVA Axis two (eigenvalue = 0.26)
CVA Axis one (eigenvalue = 0.50)

Figure 3

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

Canadian Shield lakes that are located in boreal and mixed-boreal regions, are sensitive ecosystems that have become increasingly affected by anthropogenic disturbances since pre-industrial times (Schindler, 1998). Understanding the effects of these stressors on water quality is important both to human populations, who rely on Canadian Shield lakes for drinking water and recreational purposes, and to the aquatic biological assemblages, as the ecological structure and function of these lakes may be threatened (Schindler 1997, 1998). Historical records and monitoring data are often too short in duration to assess long-term changes in water quality that are associated with these impacts. In addition to these data, paleolimnological techniques can be used to reconstruct environmental conditions prior to the onset of disturbances, to determine the timing, and possible causes of change in Ontario shield lakes.

In the four manuscripts presented in this thesis, I have used paleolimnological techniques to assess the effects of anthropogenic disturbances on the water quality of Canadian Shield lakes in Ontario, Canada. Scaled chrysophytes, which form an important part of the phytoplankton of these north-temperate lakes (Sandgren, 1988), were used as paleolimnological indicators of environmental change. These organisms are sensitive to changes in their environment (Smol, 1995a) and have been shown to respond rapidly to changes in water quality (e.g. Dixit et al., 1989). A number of important conclusions and implications, summarized below, arise from this thesis.

Logging and forest fires may only cause minimal, short-term changes in water quality

Relative to pre-disturbance conditions, lakes in northwestern Ontario showed minimal changes in water quality following the removal of greater than 90% of the watershed vegetation (Chapter 2). These disturbances were considered to be severe, having occurred in a single season, with logging and forest fires reaching the shoreline of the lakes. A number of factors may have contributed to the null response in these ecosystems. Perhaps the duration of the effect was too short to be detected at the two to four-year resolution of the sediment record. Examining streams in northwestern Ontario, Nicholson et al. (1975) determined that changes in water quality were apparent for the first three years following logging. In other studies, however, (e.g. Maine: Rhodes and Davis, 1995; Michigan: Scully et al., 2000), impacts were detected for several years to decades, and a recovery period of a century was recorded in one lake. Therefore, the question of resolution is a difficult one, as the effects may vary across lakes. Higher-resolution paleolimnological studies do exist (e.g. ~ 1-2 years: Laird and Cumming, In Press; Laird et al., In Press), but generally support the findings that these types of watershed disturbances have had minimal impacts on water quality. Moreover, additional changes apparent in the northwestern Ontario lakes, including a significant decrease in sedimentation rate in the early 1980s, suggest that other factors, related to climate, were responsible for the gradual species changes observed through time.

Watershed characteristics, such as slope, lake volume and the drainage ratio (watershed:lake area), and their effects on water residence time, are likely to be important

factors regulating the impact watershed disturbances have on aquatic ecosystems. Variability in lake morphometry may therefore result in a continuum of response to watershed disturbances among lakes and streams. At one end of this continuum are streams, as well as lakes with very large drainage areas (e.g. Mud Pond, Maine: Rhodes and Davis, 1995), small lake volumes, and consequently, low water residence times (i.e. measured in months, not years). Annual water flow to these systems, which may bring in elevated nutrient and sediment loads following a disturbance (Miller et al., 1997), will be considerably larger than to lakes with higher water residence times. Additionally, lakes with small volumes may have less of an ability to dilute the impact. However, this relationship may be complex, as rapid flushing rates in smaller lakes may also shorten the duration of the impact. At the other end of the continuum are lakes such as Lake 42 (Chapter 2), which has an estimated water residence time of approximately 10 years. The maximum annual contribution of water from the catchment will be no greater than 10% of the volume of this lake. In fact, the annual contribution will be less, as this does not consider contributions from groundwater, and from precipitation falling directly onto the lake's surface.

The above hypothesis deserves further exploration, and could be tested using a regional, fine-resolution paleolimnological approach (i.e. annual resolution). Lake selection should include sites that have experienced similar watershed disturbances (ideally the same fire or logging episode), but have varying water renewal times (which can be estimated using morphometric variables). The variability of species assemblages before and after known disturbances, and paleolimnological reconstructions of changes in

water quality (e.g. pH, nutrients, dissolved organic carbon, see Enache and Prairie, 2000), could be examined. Furthermore, paleolimnological records from flowing ecosystems are potentially possible if a suitable sedimentation basin is found (e.g. Reavie et al., 1998), and may allow for direct comparisons of the response to watershed disturbances in stream and lake ecosystems over long time periods. Such a study must be of an appropriate duration to estimate natural variability before disturbances (i.e. decades), and should include both disturbance and reference ecosystems, in order to distinguish between watershed disturbances and regional factors, such as changes in climate.

Watershed versus regional disturbances: The influence of climate

In some regions (e.g. Vancouver Island, Interior Plateau, B.C.: Laird and Cumming, 2000; Laird et al., 2000), the continuum hypothesis does not provide a suitable explanation for the minimal impacts which have been observed. Other influences, such as climate, may be of greater importance. In unusually dry years, when water flow from the catchment is reduced, the increased export of nutrients and soil detritus following a disturbance may be diminished (Schindler et al., 1996). This has important management implications, as a knowledge of past and present climate should be considered when evaluating the effects of watershed disturbance on aquatic ecosystems.

There is evidence that drought was an important factor affecting lakes during the 1970-1990 time period in northwestern Ontario. Significant changes to physical, chemical, and biological variables were detected at the Experimental Lake Area (ELA) (Schindler et al., 1990, 1996), that were more important than short-lived changes in water

quality following two watershed fires (Schindler et al., 1980). Moreover, there is evidence that this drought affected our study lakes in northwestern Ontario (Chapter 2). Significant decreases in sedimentation rate, beginning in the early 1980s, were detected in six of the eight lakes examined (Blais et al., 1998). These trends were apparent in disturbance and reference lakes, with sedimentation rates decreasing by approximately 80% in the study lakes. Similar decreases in sediment load were recorded at ELA (ca. 63% decrease), associated with a reduction in runoff from ca. 400 $mm.yr^{-1}$ to 150 $mm.yr^{-1}$, over the twenty-year drought period (Schindler et al., 1996). In northwestern Ontario, Blais et al. (1998) determined that lakes with larger drainage areas exhibited greater reductions in sedimentation rate, further illustrating the importance of hydrology in regulating watershed interactions.

An examination of scaled chrysophyte assemblages (Chapter 2) revealed subtle, gradual changes in both disturbance and reference lakes. Interestingly, species changes detected in northwestern Ontario were qualitatively similar to the changes observed in south-central Ontario. Regional shifts from an assemblage dominated by smaller, unicellular taxa (e.g. *Mallomonas deurrschmidtiae*) to larger, unicellular (e.g. *M. caudata)*, and colonial taxa (e.g. *Synura petersenii*, *S. echinulata)* were observed in both regions (Chapters 2 and 4). Although there are a number of possible explanations for the observed species trends (Chapter 5), changes in water transparency, associated with drought in northwestern Ontario (Schindler et al., 1990; Schindler et al., 1996), and the combined effects of acidification and warm temperatures in south-central Ontario (Yan et al., 1996), provide interesting possible causes for these changes. Large unicellular and

colonial chrysophytes, which have increased in abundance in the studies presented here, are commonly associated with deep-water peaks, below the thermocline (Sandgren, 1988). Increased light penetration has been shown to increase the zone of sub-thermocline production (Schindler et al., 1996), which may favour deep-water phytoplankton populations. Furthermore, unusually warm spring temperatures (Schindler et al., 1990), causing a more rapid onset of stratification, are conditions that may be conducive to the formation of chrysophyte blooms (Sandgren, 1988). Within the scaled chrysophytes, deep-blooming taxa may also gain an advantage in having reduced exposure to harmful UV-B (Xenopoulos et al., 2000), which may be of greatest threat to these spring bloomers (Smith et al., 1998a). Finally, the observed species changes were generally larger in south-central than in northwestern Ontario. This may reflect differences in the time periods examined (30-50 years in northwestern Ontario, versus > 150 years in south-central Ontario), and the influence that elevated loads of acid deposition may have on increasing water transparency (Schindler, 1997, 1998).

The Ontario Ministry of the Environment has seen an increase in taste and odour events caused by the colonial chrysophyte, *Synura petersenii* (Nicholls, 1995), although data are sketchy. These episodes have occurred in lakes spanning a wide range of water chemistry conditions, including those that are acidic or alkaline, oligotrophic or mesotrophic, and have varying disturbances in their watersheds (Nicholls and Gerath, 1985). What is presently unknown, however, is whether these events were common in the past (i.e. pre-industrial times), or are the result of anthropogenic impacts on water quality. Our findings, in a study of present-day and pre-industrial sediment samples

(Chapter 5), clearly indicate that there has been a dramatic, regional increase in taste and odour-causing chrysophytes in Ontario shield lakes. Issues of water quality, as they relate to aesthetic and health concerns, are of keen interest to the general public. However, the causative factors are presently not well understood, and therefore, this represents an interesting avenue for future research.

The existence of long-term monitoring programs (i.e. 25 years) in south-central Ontario, with continuous water chemistry data that can be compared to sedimentary species assemblages, provides an opportunity to address these questions further. New advances in multivariate statistical analysis, including variance partitioning analysis (VPA), may be used to assess the relative importance of multiple stressors on changes in water quality (e.g. Hall et al., 1999). For example, variations in species assemblages explained by changes in climate may be estimated with VPA, and contrasted with other effects, including acidic deposition (as estimated by changing sulphate loads). Furthermore, the combined influence of these impacts on biological assemblages may be calculated.

Inferred changes in lakewater pH have been small in presently circumneutral lakes

In comparison to studies in other acid-sensitive regions (e.g. the Adirondacks: Cumming et al., 1992; Sudbury: Dixit et al., 1992), that have used scaled chrysophytes as paleolimnological indicators, inferred changes in lakewater pH were small in south-central Ontario (Chapter 4). Of the 48 lakes examined, approximately 80% showed inferred changes, compared to pre-industrial times, less than the cross-validated

prediction error of the model. Similar conclusions were found using other indicators in these lakes, including diatoms (Hall and Smol, 1996) and chrysophyte cysts (Wilkinson et al., 1999). In part, these findings may be explained by the pre-industrial buffering capacities of the lakes. The Ontario lakes were relatively more buffered in comparison to many of the Adirondack lakes (Cumming et al., 1994; Smol et al., 1998), indicating that they were less susceptible to changes in pH associated with acidic deposition. The amount of acid deposition has also been lower in south-central Ontario than in other regions, such as Sudbury, Ontario (Keller et al., 1992). Finally, the lakes examined here were of a relatively narrow pH gradient, and included few very acidic lakes, that may have shown the greatest signs of acidification (e.g. Plastic Lake: Dillon et al., 1987). However, despite the relatively narrow environmental gradient (pH range: 5.61 to 7.30), pH was found to be the most important variable influencing phytoplankton distributions in present-day sediment samples (Hall and Smol, 1996; Wilkinson et al., 1999; Chapter 4).

In south-central Ontario, however, there is still cause for concern that continued deposition may adversely affect these ecosystems in the future. Despite a 35-40% reduction in sulphate deposition, beginning in the early 1980s (Dillon and LaZerte, 1992), many lakes in the region have shown no signs of recovery in pH, relative to pre-disturbance levels (Hall and Smol, 1996; Stoddard et al., 1999). A number of hypotheses, including a coincident decrease in the deposition of base cations (Hedin et al., 1994), and the depletion of cations from watershed soils (Likens et al. 1996), have been proposed. In Ontario, the re-oxidation and release of reduced sulphur stored in wetlands has also been

recognized as an important factor delaying the recovery of acidified lakes (Yan et al. 1996), which may be linked to abnormally dry periods, such as years following El Niño events (Dillon et al. 1997). These explanations suggest that the processes governing the acidification and recovery of lakes are complex, and that even with greater reductions in sulphate emissions, lake acidification will likely remain a problem in this region for several decades.

Changes in water quality in Canadian Shield lakes: General conclusions

Perhaps the most striking finding from this thesis is that changes in water quality, as inferred from scaled chrysophyte assemblages and other indicators (diatoms: Hall and Smol, 1996; Paterson et al., In Press; chrysophyte cysts: Wilkinson et al., 1999; chironomids: Quinlan, 2000; Little et al., 2000), have generally been small in these Canadian Shield lakes. Given the magnitude and number of disturbances affecting lakes within the boreal shield (Schindler, 1998), these results are unexpected. In part, watershed characteristics may regulate the impact of these disturbances in lakes. For example, the percentage of the catchment that is composed of wetlands, which may store strong acids in reduced forms (Gorham et al., 1984; LaZerte, 1993), and the depth of catchment soils, which may be indicative of the relative buffering capacity of the watershed, may be important variables influencing the magnitude of acidification that is occurring in lakes. In general, smaller lakes, with shallow soils, and a smaller percent wetland area are more susceptible to acidification (e.g. Plastic Lake, south-central Ontario: Dillon et al., 1987).

I recognize that there are limitations associated with the top-bottom paleolimnological approach used in this thesis, as it does not provide a continuous record of change between the pre-industrial and present-day time periods. However, this technique provides useful information about lakes at a regional-scale (Smol, 1995b), and has been used successfully in other studies (e.g. Cumming et al., 1992; Hall and Smol, 1996). A trade-off is often made between examining few lakes at a high-temporal resolution, or many lakes at a much coarser resolution. While we have primarily chosen the latter approach in this thesis, these techniques are complimentary, and therefore an examination of continuous sediment cores will continue to be an important direction of research in this region (e.g. Clerk et al., 2000; Little et al., 2000).

In conclusion, it is possible that the full impact of these stressors on the water quality of Canadian Shield lakes has yet to be realized. Despite a reduction in sulphate loads to lakes in south-central Ontario, many have not recovered in lakewater pH, indicating that their watershed have been severely denuded of base cations (Stoddard et al., 1999). Therefore, even under reduced loads, lakes may continue to acidify in south-central Ontario. Finally, Global Climate Models predict an increase in temperatures and the frequency of droughts in many regions of the boreal shield (Smith et al., 1998b). There are signs that the synergistic effects of acidification, climate, and increased transparency in lakes increasing harmful UV-B exposure (Xenopoulos et al., 2000) may significantly alter biological communities in Canadian Shield lakes (Leavitt et al., 1999; Yan et al., 1996). Long-term data, such as the records obtained using paleolimnological techniques, will be required to assess these changes relative to pre-disturbance (i.e. pre-

industrial) conditions, and to help predict trajectories of change in the future.

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Appendix A: Relative abundance species data from the 'reference' lakes

Lake 42 - Reference Lake
Relative abundance data

Estimated Pb-210 date	1995	1994	1993	1991	1989	1986	1983	1981
Midpoint depth (cm)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75
Taxa								
Synura petersenii	1.47	0.75	0.00	0.50	0.25	1.72	1.75	0.49
S. spinosa	23.34	19.20	23.84	22.50	18.56	18.67	25.25	22.82
S. spinosa f. longispina	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. curtispina	0.00	0.50	0.00	0.50	0.25	0.25	1.00	0.24
S. uvella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. sphagnicola	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
S. echinulata	0.00	0.00	0.49	0.25	0.00	0.00	0.00	0.00
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	5.16	4.24	2.92	5.75	5.45	4.18	3.00	2.67
M. pseudocoronata	1.72	1.25	1.95	1.25	0.99	1.23	2.00	0.97
M. caudata	13.02	9.23	9.25	11.50	15.10	12.78	12.50	11.65
M. duerrschmidtiae	25.06	29.68	26.76	23.00	29.70	30.22	26.25	36.17
M. crassisquama	4.18	5.99	5.11	5.75	5.45	9.34	6.25	3.40
M. elongata	0.25	0.00	0.00	1.50	0.00	0.25	0.50	0.24
M. hamata	7.86	9.23	13.38	11.00	8.91	8.11	7.75	10.44
M. torquata	0.49	0.50	0.49	0.50	1.24	0.49	0.50	0.97
M. punctifera	1.23	1.75	0.73	1.00	1.24	0.74	0.75	1.21
M. transsylvanica	0.49	0.75	0.73	1.25	0.99	1.47	1.50	0.73
M. galeiformis	0.98	1.50	0.97	1.75	0.99	0.00	0.50	0.24
M. allorgei	4.42	4.74	2.43	2.00	2.23	1.97	1.00	0.73
M. tonsurata	2.95	4.49	3.16	2.25	2.97	4.18	5.00	3.64
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.98	0.75	1.22	0.50	0.74	0.25	0.75	0.73
M. akrokomos	2.46	1.50	3.16	3.00	3.47	1.97	1.25	1.46
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. doignonii	0.00	0.25	0.00	1.00	0.00	0.25	0.00	0.00
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.49	0.25	0.24	0.50	0.00	0.00	0.25	0.24
Chrysosphaerella brevispina	0.74	0.50	1.22	0.50	0.25	0.49	0.75	0.24
C. longispina	1.72	2.00	0.97	1.25	0.99	0.98	0.50	0.24
Chrysodidymus synuroideus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spiniferomonas spp	0.74	1.00	0.97	0.75	0.25	0.49	0.75	0.49
Paraphysomonas spp	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00

Estimated Pb-210 date	1977	1974	1970	1965	1961	1956	1952
Midpoint depth (cm)	4.25	4.75	5.50	6.50	7.50	8.50	9.50
Taxa							
Synura petersenii	0.25	0.24	0.25	0.00	0.00	0.25	0.00
S. spinosa	32.84	29.23	33.08	30.39	28.82	31.19	24.20
S. spinosa f. longispina	0.00	0.00	0.00	0.49	0.00	0.00	0.00
S. curtispina	0.00	0.00	0.00	0.00	0.49	0.00	0.25
S. uvella	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. sphagnicola	0.00	0.00	0.25	0.00	0.25	0.00	0.00
S. echinulata	0.00	0.00	0.50	0.00	0.74	0.25	0.00
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	4.41	3.14	4.51	1.72	3.69	1.73	3.95
M. pseudocoronata	0.25	0.97	1.25	0.98	1.97	2.48	2.47
M. caudata	14.71	12.56	14.29	15.44	15.76	16.58	14.81
M. duerrschmidtiae	23.04	30.19	25.31	24.26	29.06	28.22	30.12
M. crassisquama	2.21	1.21	1.50	3.19	1.23	3.47	4.69
M. elongata	0.25	1.93	1.25	0.49	0.74	0.00	1.48
M. hamata	9.07	7.73	7.52	8.82	5.42	5.69	4.69
M. torquata	0.49	0.48	0.75	0.49	0.74	0.25	0.49
M. punctifera	0.74	0.97	0.75	0.74	0.49	1.49	0.99
M. transsylvanica	0.25	0.72	0.25	0.74	0.99	0.99	0.99
M. galeoformis	1.23	0.00	0.50	0.25	0.74	0.74	0.49
M. allorgei	0.25	0.00	0.25	0.25	0.00	0.25	0.49
M. tonsurata	4.90	4.11	2.26	3.68	3.69	2.72	4.44
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	1.47	2.17	2.01	3.43	1.97	0.99	1.48
M. akrokomas	2.70	3.14	1.25	2.45	1.48	1.24	1.48
M. heterospina	0.00	0.00	0.25	0.49	0.25	0.50	0.00
M. doignii	0.00	0.00	0.25	0.49	0.00	0.25	0.25
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.25	0.25
Chrysosphaerella brevispina	0.25	0.72	0.50	0.25	0.25	0.00	0.49
C. longspina	0.74	0.24	0.75	0.98	0.74	0.25	0.74
Chrysodidymus synuroideus	0.00	0.00	0.25	0.00	0.00	0.00	0.25
Spiniferomonas spp	0.00	0.00	0.00	0.00	0.49	0.25	0.49
Paraphysomonas spp	0.00	0.24	0.25	0.00	0.00	0.00	0.00

Appendix A (continued)

Lake 26 - Reference Lake
Relative abundance data

Estimated Pb-210 date	1995	1994	1993	1991	1989	1987	1985	1984
Midpoint depth (cm)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75
Taxa								
Synura petersenii	5.20	6.45	6.45	4.33	6.68	6.01	7.00	14.00
S. spinosa	9.16	12.41	14.89	34.13	35.64	27.88	25.25	18.43
S. spinosa f. longispina	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00
S. curtispina	11.39	10.67	7.69	2.64	0.99	1.44	1.50	0.25
S. uvella	0.00	0.25	0.25	0.00	0.00	0.24	0.00	0.00
S. sphagnicola	0.25	0.00	0.00	0.00	0.00	0.24	0.00	0.74
S. echinulata	2.97	1.49	0.99	0.96	0.50	0.48	0.25	0.49
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	2.23	5.96	2.23	2.40	1.98	2.40	1.75	1.97
M. pseudocoronata	3.96	4.96	2.23	3.37	3.47	4.57	3.00	3.19
M. caudata	10.89	10.92	10.67	8.89	9.41	10.82	9.75	7.62
M. duerrschmidtiae	12.87	10.67	16.63	9.62	10.15	11.78	12.50	18.67
M. crassisquama	1.49	0.00	0.99	0.48	0.50	2.16	0.75	1.23
M. elongata	0.99	0.74	1.99	0.48	0.74	0.72	0.50	0.98
M. hamata	17.08	16.38	19.60	18.03	15.35	17.07	21.50	18.18
M. torquata	0.74	0.25	0.00	0.00	0.25	0.00	0.00	0.00
M. punctifera	1.49	1.49	0.99	1.20	0.50	1.92	3.00	1.47
M. transsylvanica	5.20	4.96	3.47	2.16	2.48	2.40	2.00	2.21
M. galeiformis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. allorgei	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. tonsurata	0.50	0.74	0.99	0.72	0.50	0.00	1.00	0.49
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	2.48	3.47	2.73	0.96	2.72	2.16	1.25	3.19
M. akrokomos	3.47	2.98	1.49	4.57	3.22	2.88	3.75	3.93
M. heterospina	0.00	0.74	1.24	0.00	0.00	0.48	1.00	0.25
M. doignonii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chrysosphaerella brevispina	2.23	1.24	1.24	1.68	0.74	1.20	1.75	0.74
C. longispina	4.70	1.99	1.49	2.40	3.22	1.20	1.75	0.98
Chrysodidymus synuroideus	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00
Spiniferomonas spp	0.50	1.24	1.74	0.96	0.74	1.44	0.75	0.49
Paraphysomonas spp	0.25	0.00	0.00	0.00	0.25	0.00	0.00	0.25

Estimated Pb-210 date	1982	1980	1978	1975	1971	1966	1961
Midpoint depth (cm)	4.25	4.75	5.50	6.50	7.50	8.50	9.50
Taxa							
Synura petersenii	8.80	5.25	6.95	6.75	5.85	7.69	7.73
S. spinosa	16.38	17.13	19.85	17.75	19.67	18.27	17.63
S. spinosa f. longispina	0.00	0.00	0.00	0.00	0.47	0.72	0.00
S. curtispina	0.98	0.55	0.50	0.25	0.70	0.24	0.48
S. uvella	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. sphagnicola	0.00	0.00	0.00	0.50	0.00	0.00	0.00
S. echinulata	0.00	0.28	0.25	0.00	0.00	0.48	0.00
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.24	0.24
Mallomonas SMALL	1.22	1.66	2.73	2.50	7.03	6.25	6.52
M. pseudocoronata	7.33	7.46	5.96	9.75	7.03	6.01	8.45
M. caudata	7.82	8.01	7.69	6.50	5.85	4.09	4.11
M. duerrschmidtiae	27.87	27.35	26.80	30.75	29.74	30.53	29.23
M. crassisquama	2.69	3.59	2.23	0.75	1.87	1.20	2.42
M. elongata	0.49	0.55	1.24	0.25	0.00	0.24	0.48
M. hamata	13.20	14.92	14.39	13.00	11.24	10.10	9.66
M. torquata	0.24	0.28	0.25	0.00	0.47	0.24	0.48
M. punctifera	1.47	1.10	0.50	2.00	0.70	1.68	1.21
M. transsylvanica	3.18	1.66	0.74	1.50	1.64	1.68	2.17
M. galeoformis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. allorgei	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. tonsurata	0.49	0.00	0.50	0.25	0.70	0.48	0.24
M. acaroides f. muskokana	0.24	0.00	0.00	0.00	0.23	0.72	0.48
M. MEDIUM	2.93	3.31	2.73	3.50	2.81	3.85	5.31
M. akrokomas	0.73	1.93	2.48	1.25	0.94	1.44	0.72
M. heterospina	0.73	0.28	0.00	1.00	0.00	0.24	0.00
M. doignii	0.00	0.00	0.00	0.00	0.23	0.48	0.97
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chrysosphaerella brevispina	1.47	2.21	1.49	0.25	0.23	0.48	0.00
C. longspina	1.47	2.21	2.23	1.25	0.94	0.96	0.97
Chrysodidymus synuroideus	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spiniferomonas spp	0.24	0.28	0.50	0.25	0.23	1.20	0.24
Paraphysomonas spp	0.00	0.00	0.00	0.00	1.41	0.48	0.24

Appendix B: Relative abundance species data from the 'burn' lakes

BN1 - Burn Lake
Relative abundance data

Estimated Pb-210 date	1995	1993	1991	1988	1984	1981	1978	1975
Midpoint depth (cm)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75
Taxa								
Synura petersenii	7.96	9.46	8.01	3.44	3.25	3.42	5.41	2.67
S. spinosa	0.25	0.24	0.49	0.00	0.25	0.00	0.25	0.24
S. spinosa f. longispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. curtispina	0.00	0.47	0.24	0.25	0.25	0.00	0.25	0.24
S. uvella	1.99	1.18	0.73	1.72	2.25	1.22	1.97	1.70
S. sphagnicola	33.58	34.52	33.98	25.31	24.50	26.89	25.31	18.93
S. echinulata	4.48	3.78	2.43	1.23	1.50	3.18	1.97	1.94
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	5.47	4.02	2.43	2.95	2.25	2.20	4.18	3.40
M. pseudocoronata	7.96	5.20	7.52	9.09	7.00	9.78	6.39	5.10
M. caudata	3.23	4.73	3.40	4.67	5.50	3.42	4.18	5.10
M. duerrschmidtiae	5.47	7.80	8.25	16.71	16.25	10.76	13.27	19.66
M. crassisquama	7.21	7.57	11.41	15.23	15.75	15.65	13.51	17.48
M. elongata	0.75	0.00	0.24	0.25	0.50	0.73	0.25	0.49
M. hamata	1.74	2.13	1.46	1.72	3.00	5.38	4.18	4.37
M. torquata	0.75	0.00	0.00	0.00	0.50	0.24	0.74	0.00
M. punctifera	0.00	0.00	0.00	1.23	0.25	0.49	0.98	0.73
M. trannsylvanica	0.25	0.24	0.73	0.49	0.50	0.49	0.49	0.73
M. galeiformis	0.00	0.24	0.00	0.00	0.00	0.00	0.98	0.00
M. allorgei	0.00	0.00	0.00	0.25	0.75	0.49	0.00	0.49
M. tonsurata	0.75	0.24	0.24	0.49	1.25	1.96	2.70	2.91
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	1.00	1.42	0.97	2.21	1.00	0.73	0.25	0.73
M. akrokomos	0.00	0.00	0.49	0.00	0.50	0.24	0.00	0.00
M. heterospina	0.00	0.00	0.00	0.49	0.25	0.24	0.00	0.00
M. doignonii	0.00	0.00	0.24	0.25	0.00	0.00	0.00	0.00
M. insignis	0.00	0.00	0.00	0.00	0.00	0.24	1.72	0.24
M. lelymene	0.25	0.95	0.97	0.74	0.25	0.49	0.98	1.70
Chrysosphaerella brevispina	4.73	3.31	4.13	1.97	2.50	2.44	2.21	1.70
C. longispina	10.20	10.64	9.71	7.86	8.25	7.82	6.63	8.25
Chrysodidymus synuroideus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spiniferomonas spp	1.74	1.89	1.94	1.47	1.50	1.22	1.23	0.97
Paraphysomonas spp	0.25	0.00	0.00	0.00	0.25	0.24	0.00	0.24

Estimated Pb-210 date	1972	1969	1968	1963	1957	1951	1943
Midpoint depth (cm)	4.25	4.75	5.50	6.50	7.50	8.50	9.50
Taxa							
Synura petersenii	1.98	3.33	3.95	4.31	3.47	3.25	2.43
S. spinosa	0.00	0.24	0.00	0.24	0.25	0.25	0.00
S. spinosa f. longispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. curtispina	0.00	0.00	0.49	0.24	0.00	0.00	0.24
S. uvella	2.22	0.24	2.47	1.20	1.74	1.25	1.46
S. sphagnicola	20.74	26.37	18.52	20.10	16.87	15.25	16.99
S. echinulata	1.98	1.66	1.98	1.44	1.24	1.00	0.24
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	2.72	4.99	4.69	3.35	3.47	4.00	2.91
M. pseudocoronata	9.14	6.18	7.65	5.26	6.95	6.75	8.25
M. caudata	5.19	2.14	3.46	4.07	4.22	3.00	4.37
M. duerrschmidtiae	21.73	19.00	23.21	23.21	26.30	29.00	30.83
M. crassisquama	15.06	10.93	14.07	11.00	11.66	9.00	8.74
M. elongata	0.00	0.00	0.00	0.24	0.50	0.25	0.49
M. hamata	4.44	4.51	2.72	3.59	3.72	4.25	4.61
M. torquata	0.49	0.95	0.25	0.00	0.74	0.00	0.24
M. punctifera	0.74	0.71	0.99	1.20	0.99	0.75	0.73
M. trannsylvanica	0.00	0.48	0.00	0.48	0.50	0.75	0.73
M. galeoformis	0.49	0.00	0.49	0.48	0.50	0.50	0.49
M. allorgei	0.74	0.48	1.98	0.72	1.24	1.25	1.70
M. tonsurata	2.72	2.61	3.95	3.11	2.23	2.25	3.16
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.74	0.95	1.23	1.91	0.25	2.00	0.73
M. akrokomas	0.00	0.24	0.00	0.00	0.50	0.50	0.24
M. heterospina	0.00	0.00	0.25	0.00	0.00	0.00	0.00
M. doignii	0.00	0.24	0.00	0.00	0.00	0.00	0.24
M. insignis	0.00	0.48	0.00	0.00	0.25	0.25	0.00
M. lelymene	1.23	0.71	1.23	0.96	0.99	0.50	0.24
Chrysosphaerella brevispina	0.49	2.14	0.74	1.91	1.49	2.25	1.46
C. longspina	6.17	8.08	5.43	9.57	7.94	10.25	7.52
Chrysodidymus synuroideus	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spiniferomonas spp	0.74	2.14	0.25	1.44	1.74	1.50	0.97
Paraphysomonas spp	0.25	0.24	0.00	0.00	0.25	0.00	0.00

Appendix B (continued)

BN2 - Burn Lake
Relative abundance data

Estimated Pb-210 date	1995	1994.6	1994	1993	1992	1991	1990	1989
Midpoint depth (cm)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75
Taxa								
Synura petersenii	14.96	15.63	10.46	12.65	11.92	10.41	13.47	12.50
S. spinosa	0.50	0.25	0.73	0.48	0.73	0.00	0.23	1.25
S. spinosa f. longispina	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00
S. curtispina	0.00	0.00	0.00	0.00	0.00	0.48	0.00	0.00
S. uvella	2.74	1.74	2.43	0.24	1.70	2.66	3.20	1.75
S. sphagnicola	4.99	5.46	6.57	5.01	6.81	8.47	4.79	8.75
S. echinulata	31.92	25.81	31.87	29.83	31.63	30.02	33.33	31.75
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	2.74	3.97	1.70	2.39	1.46	4.36	4.57	2.50
M. pseudocoronata	5.24	5.71	5.11	3.34	5.35	3.87	3.65	3.50
M. caudata	4.74	4.22	3.65	4.06	4.38	3.87	2.97	2.00
M. duerrschmidtiae	2.00	3.23	2.68	2.86	5.60	2.42	1.37	2.50
M. crassisquama	8.48	7.44	9.00	9.31	9.25	8.47	7.08	8.00
M. elongata	0.00	0.50	0.49	0.00	0.00	0.00	0.00	0.00
M. hamata	2.00	1.74	4.14	2.39	1.46	3.87	2.97	3.50
M. torquata	0.00	0.00	0.00	0.72	0.00	0.24	0.23	0.00
M. punctifera	0.00	0.00	0.24	0.24	0.24	0.00	0.00	0.00
M. transsylvanica	0.00	0.25	0.00	0.00	0.00	0.24	0.68	0.00
M. galeriformis	0.00	0.50	0.00	0.00	0.24	0.00	0.00	0.00
M. allorgei	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00
M. tonsurata	0.50	0.25	0.49	1.19	1.22	1.94	0.91	0.75
M. acaroides f. muskokana	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.00	0.50	0.49	0.48	0.49	0.48	0.23	0.00
M. akrokomos	0.75	1.24	0.49	0.24	0.97	1.45	0.46	1.25
M. heterospina	0.50	0.25	0.00	0.24	0.97	0.24	0.00	0.25
M. doignonii	0.00	0.00	0.24	0.00	0.49	0.00	0.00	0.00
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chrysosphaerella brevispina	4.99	4.22	4.62	5.01	3.16	2.18	4.79	4.50
C. longispina	11.47	15.38	13.14	17.42	11.44	12.11	14.38	12.75
Chrysodidymus synuroideus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.50
Spiniferomonas spp	0.50	1.24	0.73	1.67	0.24	1.21	0.00	0.50
Paraphysomonas spp	0.50	0.50	0.73	0.24	0.24	0.73	0.46	0.50

Estimated Pb-210 date	1988	1986	1985	1982	1979	1975	1972
Midpoint depth (cm)	4.25	4.75	5.50	6.50	7.50	8.50	9.50
Taxa							
Synura petersenii	13.97	10.10	14.39	10.54	8.89	15.71	15.76
S. spinosa	0.75	1.23	0.99	1.47	0.49	0.50	0.24
S. spinosa f. longispina	0.00	0.00	0.00	0.25	0.00	0.00	0.00
S. curtispina	0.00	0.25	0.00	0.00	0.25	0.00	0.24
S. uvella	1.50	2.22	1.24	1.23	0.99	2.00	0.94
S. sphagnicola	8.73	5.42	4.47	6.37	6.17	6.23	6.12
S. echinulata	29.93	37.93	34.99	31.62	32.35	31.67	30.82
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	1.00	2.96	1.49	1.23	2.96	2.00	2.82
M. pseudocoronata	3.74	6.16	3.97	5.64	4.20	3.24	5.88
M. caudata	3.49	6.16	5.71	4.90	3.46	1.50	5.88
M. duerrschmidtiae	3.24	2.71	2.48	3.19	3.46	2.49	2.12
M. crassisquama	5.99	11.82	10.42	13.24	10.86	6.73	9.65
M. elongata	0.25	0.00	0.25	0.00	0.00	0.00	0.00
M. hamata	3.74	1.72	3.97	4.17	3.46	4.99	1.65
M. torquata	0.00	0.00	0.00	0.25	0.49	0.25	0.00
M. punctifera	0.50	0.00	0.00	0.25	0.00	0.00	0.24
M. transsylvanica	0.00	0.25	0.00	0.25	0.00	0.00	0.00
M. galeoformis	0.25	0.00	0.50	0.25	0.00	0.25	0.24
M. allorgei	0.00	0.25	0.00	0.00	0.00	0.00	0.00
M. tonsurata	1.25	0.99	0.99	0.74	1.48	1.00	0.24
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	1.00	0.49	1.49	0.74	1.23	0.25	0.00
M. akrokomas	0.00	0.00	1.24	0.00	0.99	0.00	0.24
M. heterospina	0.00	0.00	0.50	0.00	0.25	0.25	0.00
M. doignii	0.25	0.00	0.00	0.00	0.25	0.00	0.00
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chrysosphaerella brevispina	4.24	1.48	3.23	4.17	3.46	6.73	3.76
C. longspina	14.96	7.14	7.44	9.07	12.84	13.47	10.82
Chrysodidymus synuroideus	0.75	0.25	0.00	0.00	0.00	0.00	0.47
Spiniferomonas spp	0.50	0.49	0.25	0.49	0.99	0.75	0.94
Paraphysomonas spp	0.00	0.00	0.00	0.00	0.49	0.00	0.94

Appendix C: Relative abundance species data from the 'cut' lakes

M6N - Cut Lake
Relative abundance data

Estimated Pb-210 date	1995	1994.5	1994	1992	1991	1990	1989	1988
Midpoint depth (cm)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75
Taxa								
Synura petersenii	17.92	22.77	30.40	19.91	20.40	19.77	13.11	14.60
S. spinosa	2.18	1.64	0.95	1.66	2.74	2.33	1.46	0.74
S. spinosa f. longispina	0.00	0.23	0.00	0.24	0.00	0.23	0.00	0.00
S. curtispina	0.24	0.47	0.71	0.47	0.00	0.00	0.49	0.25
S. uvella	2.91	0.94	2.61	3.79	3.23	2.33	2.91	2.48
S. sphagnicola	12.59	15.73	15.91	13.27	18.91	15.81	13.59	14.36
S. echinulata	13.32	11.27	9.50	5.21	7.46	6.74	6.07	4.95
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	2.42	2.11	2.14	3.08	2.49	1.63	1.70	0.74
M. pseudocoronata	1.94	1.64	1.90	1.18	1.24	2.56	2.91	1.98
M. caudata	4.12	3.05	3.80	5.21	6.72	6.74	7.04	8.42
M. duerrschmidtiae	10.17	9.15	10.45	21.09	14.93	16.74	25.97	24.75
M. crassisquama	5.57	6.57	8.08	14.69	5.72	11.40	7.52	9.16
M. elongata	0.00	0.00	0.24	0.47	0.50	0.00	0.24	0.50
M. hamata	3.15	3.52	0.95	2.84	3.98	2.56	4.37	3.22
M. torquata	0.48	0.47	0.71	0.47	0.25	0.47	0.73	0.99
M. punctifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. transsylvanica	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.50
M. galeiformis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. allorgei	0.00	0.23	0.00	0.00	0.00	0.47	0.49	0.25
M. tonsurata	0.73	0.00	0.24	0.00	1.00	1.63	0.49	0.25
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.24	0.23	0.00	0.24	0.00	0.47	0.24	0.25
M. akrokomos	0.24	0.47	0.48	0.47	0.50	0.70	0.49	0.00
M. heterospina	0.73	0.00	0.24	0.00	0.00	0.23	0.24	0.74
M. doignonii	0.00	0.00	0.48	0.00	0.00	0.00	0.00	0.00
M. insignis	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Chrysosphaerella brevispina	4.84	3.76	1.90	0.47	1.74	0.93	1.21	3.22
C. longispina	15.25	15.02	6.89	4.03	7.71	5.35	8.01	7.18
Chrysodidymus synuroideus	0.24	0.00	0.00	0.00	0.25	0.00	0.00	0.00
Spiniferomonas spp	0.73	0.47	0.48	1.18	0.25	0.93	0.49	0.25
Paraphysomonas spp	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.00

Estimated Pb-210 date	1986	1985	1984	1981	1979	1978	1976
Midpoint depth (cm)	4.25	4.75	5.50	6.50	7.50	8.50	9.50
Taxa							
Synura petersenii	18.36	13.38	20.10	15.71	13.93	8.35	5.24
S. spinosa	2.23	3.16	4.71	2.49	1.49	0.95	1.00
S. spinosa f. longispina	0.00	0.00	0.25	0.00	0.00	0.00	0.00
S. curtispina	0.25	0.24	0.25	0.00	0.25	0.00	0.00
S. uvella	2.23	2.43	2.23	2.00	1.24	1.19	1.50
S. sphagnicola	13.65	10.71	11.66	13.97	15.67	17.42	15.96
S. echinulata	8.93	9.00	9.68	9.48	5.22	1.19	2.99
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	0.50	2.43	3.47	1.50	1.99	2.15	1.25
M. pseudocoronata	2.73	3.65	1.99	2.00	2.49	4.06	5.49
M. caudata	4.71	3.89	2.48	5.49	5.72	8.59	9.98
M. duerrschmidtiae	22.58	27.49	19.60	25.44	27.11	34.84	30.42
M. crassisquama	5.21	10.22	6.45	6.98	9.95	6.44	8.98
M. elongata	0.00	0.24	0.00	0.00	0.00	0.00	0.00
M. hamata	3.97	4.62	3.23	3.99	4.98	5.25	4.74
M. torquata	0.00	0.97	0.00	0.25	0.25	0.24	0.00
M. punctifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. transsylvanica	0.25	0.00	0.00	0.25	0.00	0.00	0.00
M. galeoformis	0.25	0.00	0.00	0.00	0.25	0.00	0.25
M. allorgei	0.00	0.24	0.25	0.50	0.50	0.48	1.50
M. tonsurata	0.50	0.49	0.50	0.25	1.00	0.95	0.75
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.25	0.49	0.25	0.00	0.25	0.24	0.75
M. akrokomas	0.50	1.46	1.74	1.00	0.25	0.48	0.75
M. heterospina	0.25	0.24	0.00	0.25	0.00	0.24	0.00
M. doignii	0.00	0.00	0.00	0.00	0.25	0.00	0.25
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.24	0.25
Chrysosphaerella brevispina	1.49	1.22	2.23	2.24	1.99	1.67	2.74
C. longspina	10.67	2.68	8.19	5.24	4.48	3.10	3.24
Chrysodidymus synuroideus	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spiniferomonas spp	0.50	0.73	0.74	1.00	0.75	1.43	2.00
Paraphysomonas spp	0.00	0.00	0.00	0.00	0.00	0.48	0.00

Appendix C (continued)

M6S - Cut Lake
Relative abundance data

Estimated Pb-210 date	1995	1994	1991	1989	1987	1985	1982	1980
Midpoint depth (cm)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75
Taxa								
Synura petersenii	24.64	20.44	26.35	12.38	9.18	8.96	9.22	7.00
S. spinosa	1.44	1.97	1.48	0.73	0.24	1.21	0.24	0.50
S. spinosa f. longispina	0.00	0.00	0.00	0.24	0.00	0.00	0.00	0.00
S. curtispina	0.24	0.00	0.00	0.24	0.00	0.00	0.00	0.00
S. uvella	2.39	2.46	0.99	1.70	1.45	0.73	0.95	1.25
S. sphagnicola	12.68	10.59	13.55	16.02	13.53	16.22	20.09	19.00
S. echinulata	6.46	5.17	5.91	6.31	2.90	2.18	2.36	2.50
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	2.39	0.00	3.69	0.97	2.17	1.94	4.26	3.75
M. pseudocoronata	2.63	5.17	1.72	4.61	3.62	7.02	2.60	3.75
M. caudata	3.59	6.16	4.68	8.25	6.04	6.30	8.27	5.75
M. duerrschmidtiae	17.94	22.41	15.52	20.39	32.13	29.78	27.66	28.75
M. crassisquama	7.42	8.13	2.46	8.01	11.35	8.47	7.09	11.00
M. elongata	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. hamata	3.11	2.96	4.68	6.07	3.62	5.81	5.44	7.25
M. torquata	0.24	0.25	0.49	0.00	0.72	0.97	0.71	0.00
M. punctifera	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00
M. transylvanica	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. galeiformis	0.24	0.00	0.00	0.24	0.00	0.00	0.00	0.00
M. allorgei	0.24	0.00	0.25	0.24	0.97	0.00	1.18	0.00
M. tonsurata	0.72	0.99	0.49	0.00	0.48	0.24	0.24	0.50
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.48	0.25	0.00	0.24	0.00	0.00	0.24	0.50
M. akrokomos	0.96	1.23	1.23	0.49	0.72	0.24	0.47	0.25
M. heterospina	0.00	0.00	0.25	0.49	0.00	0.24	0.00	0.00
M. doignonii	0.00	0.25	0.25	0.24	0.00	0.00	0.47	0.00
M. insignis	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00
Chrysosphaerella brevispina	2.39	3.20	4.43	3.40	3.62	2.66	2.84	2.25
C. longispina	6.94	6.65	8.87	6.55	5.56	5.08	3.78	5.25
Chrysodidymus synuroideus	0.48	0.25	0.49	0.24	0.00	0.00	0.24	0.25
Spiniferomonas spp	1.67	1.48	1.72	1.94	1.45	1.69	1.65	0.25
Paraphysomonas spp	0.00	0.00	0.25	0.00	0.24	0.00	0.00	0.25

Estimated Pb-210 date	1977	1973	1970	1967	1963	1957	1952
Midpoint depth (cm)	4.25	4.75	5.50	6.50	7.50	8.50	9.50
Taxa							
Synura petersenii	7.62	11.14	8.98	10.80	6.73	10.70	8.56
S. spinosa	0.49	1.24	1.25	0.50	0.75	0.25	0.73
S. spinosa f. longispina	0.00	0.00	0.25	0.00	0.00	0.00	0.00
S. curtispina	0.00	0.25	0.00	0.00	0.00	0.25	0.49
S. uvella	1.72	1.24	1.00	2.26	1.50	1.24	1.71
S. sphagnicola	14.50	18.81	13.97	17.34	15.46	13.43	12.96
S. echinulata	3.44	2.23	2.24	2.26	2.24	2.24	2.69
S. lapponica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.00	0.00	0.24
Mallomonas SMALL	2.95	1.73	2.74	2.26	2.74	2.74	1.96
M. pseudocoronata	3.69	2.72	3.74	3.02	2.74	6.97	3.91
M. caudata	6.39	6.19	5.74	6.78	5.49	6.47	6.36
M. duerrschmidtiae	31.70	35.64	38.40	36.43	38.15	31.09	35.94
M. crassisquama	11.06	7.67	7.48	7.29	4.99	8.71	7.58
M. elongata	0.49	0.00	0.00	0.00	0.00	0.00	0.49
M. hamata	6.14	5.94	5.74	4.27	9.48	6.72	7.58
M. torquata	0.25	0.25	0.25	0.25	0.00	0.25	0.00
M. punctifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. transylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. galeoformis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. allorgei	1.23	0.25	2.00	0.50	1.25	1.49	1.96
M. tonsurata	0.00	0.25	0.25	0.50	0.25	0.25	0.49
M. acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.00	0.00	0.00	0.00	0.00	0.25	0.00
M. akrokomas	0.25	0.25	0.50	0.00	1.75	1.49	0.73
M. heterospina	0.00	0.00	0.25	0.25	0.00	0.25	0.00
M. doignii	0.00	0.25	0.00	0.25	0.00	0.00	0.00
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	1.01	0.00	0.25	0.00
Chrysosphaerella brevispina	2.95	1.49	1.75	0.75	1.00	0.50	1.71
C. longspina	3.69	1.24	2.24	2.01	2.24	1.74	1.47
Chrysodidymus synuroideus	0.00	0.25	0.00	0.00	0.00	0.25	0.00
Spiniferomonas spp	1.23	0.74	1.00	1.01	2.49	2.49	2.44
Paraphysomonas spp	0.25	0.25	0.25	0.25	0.75	0.00	0.00

Appendix C (continued)

M4W - Cut Lake
Relative Abundance Data

Estimated Pb-210 date	1995	1994	1993	1991	1990	1988	1987	1985
Midpoint depth (cm)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75
Taxa								
Synura petersenii	10.12	8.17	4.09	3.97	5.21	3.72	2.74	6.22
S. spinosa	3.95	2.64	1.68	2.73	2.48	1.74	1.00	0.75
S. spinosa f. longispina	1.73	1.44	0.72	0.25	0.74	0.50	0.00	0.25
S. curtispina	0.00	0.24	0.48	0.25	0.25	0.25	0.25	0.00
S. uvella	1.73	1.20	0.72	0.74	0.74	0.74	0.75	1.00
S. sphagnicola	32.84	29.57	29.33	32.75	33.00	33.00	27.68	23.13
S. echinulata	9.63	18.03	18.27	15.88	15.38	13.40	13.22	14.93
S. lapponica	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. mollispina	0.00	0.24	0.24	0.00	0.00	0.00	0.00	0.00
Mallomonas SMALL	6.17	4.09	6.01	3.97	5.21	3.72	5.74	5.22
M. pseudocoronata	0.25	0.00	0.24	0.25	0.25	0.99	1.25	1.00
M. caudata	2.22	2.40	3.85	2.98	3.97	6.70	3.99	4.48
M. duerrschmidtiae	1.98	5.29	5.53	6.95	6.20	5.46	6.73	7.71
M. crassisquama	5.43	6.49	9.38	8.19	8.68	10.17	8.73	8.71
M. elongata	0.49	0.48	0.00	0.00	0.25	0.00	0.00	0.25
M. hamata	0.00	0.96	1.44	1.49	2.73	1.99	1.75	1.49
M. torquata	3.95	2.64	1.44	1.24	2.23	1.24	2.24	2.74
M. punctifera	0.74	0.00	0.00	0.00	0.00	0.25	0.00	0.00
M. transsylvanica	1.48	0.24	0.72	0.74	0.74	1.74	2.00	1.74
M. galeiformis	0.49	0.00	0.48	0.25	0.00	0.00	0.25	0.00
M. allorgei	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00
M. tonsurata	1.23	2.40	1.44	2.23	1.24	0.74	3.49	1.49
M. acaroides f. muskokana	0.25	0.72	0.96	1.49	0.25	1.99	0.50	1.00
M. MEDIUM	0.25	0.48	0.96	0.25	0.74	0.50	0.75	0.50
M. akrokomos	0.99	0.24	0.24	0.00	0.25	0.50	0.75	0.00
M. heterospina	0.25	0.24	0.96	0.00	0.25	0.74	0.25	0.50
M. doignonii	0.25	0.24	0.00	0.25	0.00	0.25	0.25	0.50
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chrysosphaerella brevispina	2.72	4.09	2.40	2.48	1.24	1.99	1.00	2.49
C. longispina	8.40	5.77	6.01	9.68	6.20	7.20	13.22	12.44
Chrysodidymus synuroideus	0.49	0.24	0.96	0.00	0.25	0.00	0.00	0.00
Spiniferomonas spp	1.23	1.44	1.20	0.74	1.24	0.50	0.75	1.49
Paraphysomonas spp	0.49	0.00	0.00	0.25	0.25	0.00	0.75	0.00

Estimated Pb-210 date	1984	1982	1979	1975	1971	1966	1961
Midpoint depth (cm)	4.25	4.75	5.50	6.50	7.50	8.50	9.50
Taxa							
Synura petersenii	3.89	8.46	4.74	7.35	6.73	3.19	2.24
S. spinosa	0.97	1.24	1.50	1.23	1.68	0.25	0.50
S. spinosa f. longispina	0.00	0.25	0.00	0.25	0.48	0.00	0.00
S. curtispina	0.00	0.00	0.00	0.00	0.24	0.00	0.00
S. uvella	0.97	0.50	1.50	1.96	1.20	0.98	1.24
S. sphagnicola	27.49	30.85	25.69	24.02	24.28	24.32	35.07
S. echinulata	14.11	12.94	14.71	15.20	11.54	11.06	9.45
S. lapponica	0.00	0.00	0.00	0.25	0.00	0.00	0.00
S. mollispina	0.00	0.00	0.00	0.00	0.24	0.00	0.00
Mallomonas SMALL	6.33	4.98	3.99	6.37	4.57	4.42	6.47
M. pseudocoronata	0.49	1.00	0.00	0.74	0.48	2.21	1.24
M. caudata	6.08	6.22	4.99	2.94	6.01	7.62	4.98
M. duerrschmidtiae	7.79	2.99	6.48	3.92	8.89	14.00	8.46
M. crassisquama	7.79	8.71	13.47	12.01	17.07	15.72	11.44
M. elongata	0.00	0.00	0.00	0.25	0.00	0.25	0.00
M. hamata	3.16	1.24	2.00	0.98	0.72	1.97	1.49
M. torquata	2.43	1.99	2.49	2.45	1.92	0.49	3.48
M. punctifera	0.00	0.00	0.00	0.25	0.48	0.00	0.00
M. transsylvanica	1.22	2.24	0.25	0.74	0.48	0.49	1.00
M. galeoformis	0.00	0.25	0.50	0.00	0.00	0.25	0.00
M. allorgei	0.00	0.25	0.00	0.00	0.00	0.49	0.00
M. tonsurata	2.43	1.49	1.50	2.94	2.16	1.47	3.73
M. acaroides f. muskokana	0.49	0.00	0.50	0.25	0.24	0.25	0.25
M. MEDIUM	0.73	0.75	0.25	0.98	1.44	1.97	1.24
M. akrokomas	0.00	0.25	0.50	0.25	0.00	0.25	0.75
M. heterospina	0.00	0.25	0.00	0.25	0.00	0.25	0.00
M. doignii	0.00	0.25	0.25	0.00	0.00	0.25	0.25
M. insignis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chrysosphaerella brevispina	1.46	2.49	2.49	4.41	0.48	2.21	2.24
C. longspina	10.95	8.46	10.97	8.33	7.45	4.18	3.48
Chrysodidymus synuroideus	0.24	0.00	0.00	0.00	0.00	0.00	0.25
Spiniferomonas spp	0.97	1.74	0.50	1.47	1.20	1.23	0.50
Paraphysomonas spp	0.00	0.25	0.75	0.25	0.00	0.25	0.25

Appendix D: Relative abundance species data from 53 present-day sediment samples

Muskoka-Haliburton (Tops)
Relative abundance data

	12 Mile	Bass	Basshaunt	Bigwind	Blue Chalk	Boshkung	Bruce	Buck
Taxa								
Mallomonas acaroides f. muskokana	0.00	0.61	0.00	0.00	0.00	0.00	0.25	0.00
M. akrokomos	0.70	0.61	0.49	0.00	1.47	0.25	0.25	2.24
M. caudata	1.64	0.92	1.71	4.44	19.56	0.99	7.46	7.46
M. crassisquama	9.81	2.75	13.90	4.20	1.71	17.62	15.67	12.19
M. duerrschmidtiae	0.47	0.92	0.24	7.65	2.69	1.49	0.50	2.49
M. elongata	1.17	0.00	0.00	0.49	0.24	1.24	0.50	2.49
M. galeiformis	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.25
M. hamata	1.87	0.31	2.20	4.20	3.67	3.23	0.25	8.71
M. heterospina	0.23	0.31	0.00	0.25	0.24	0.00	0.00	2.49
M. lelymene	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00
M. lychenensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. MEDIUM	0.47	0.00	0.24	0.00	0.00	1.74	0.00	1.24
M. pseudocoronata	2.10	1.83	0.98	5.68	1.71	6.45	0.25	0.25
M. punctifera	0.70	0.00	0.00	0.00	0.49	0.00	0.00	2.74
M. SMALL	0.23	2.14	0.98	0.49	0.24	1.74	0.25	0.50
M. tonsurata	0.47	1.83	0.24	0.25	0.98	0.25	0.25	0.00
M. torquata	0.70	0.00	0.00	0.25	0.24	1.49	2.24	1.24
M. transsylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Synura curtispina	2.34	0.61	0.49	0.00	1.71	2.98	0.25	0.50
S. echinulata	27.34	6.12	11.22	0.99	2.20	40.45	6.22	2.74
S. petersenii	11.92	18.04	30.24	42.96	51.10	12.41	13.68	1.00
S. sphagnicola	0.70	37.00	23.90	19.51	0.00	0.99	40.30	0.25
S. spinosa	5.37	2.75	5.37	4.69	4.89	3.47	2.99	14.43
S. uvella	2.80	1.83	1.71	1.98	5.38	0.74	3.23	32.84
Chrysosphaerella spp	1.40	19.57	5.85	1.98	0.98	0.99	3.73	2.24
Paraphysomonas spp	0.70	0.61	0.00	0.00	0.00	0.25	1.24	0.00
Spiniferomonas spp	2.34	0.92	0.00	0.00	0.24	0.99	0.25	1.00

	Butterfly	Canning	Chub	Clear	Crosson	Dickie	Eagle	Frazer Island
Taxa								
Mallomonas acaroides f. muskokana	0.00	0.00	3.23	0.25	0.98	2.74	0.00	0.00
M. akrokomos	0.73	0.48	0.00	0.49	0.00	0.75	0.75	0.49
M. caudata	6.81	6.97	2.74	7.86	0.98	2.24	2.99	0.25
M. crassisquama	21.17	13.94	0.75	5.41	0.73	2.00	10.70	8.58
M. duerrschmidtiae	0.49	0.24	2.24	34.15	1.71	4.24	0.25	28.19
M. elongata	0.00	0.72	1.00	0.49	0.00	0.00	0.50	0.25
M. galeiformis	0.00	0.00	0.25	1.23	0.00	0.50	0.00	0.49
M. hamata	0.24	0.72	0.00	2.70	0.73	1.25	5.47	6.13
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	1.47	0.00	0.00	0.00	0.00
M. lychenensis	0.00	0.00	0.00	4.18	0.00	0.25	0.00	0.74
M. MEDIUM	0.97	2.16	0.00	0.49	0.00	0.25	0.25	0.74
M. pseudocoronata	2.19	3.85	0.50	1.72	0.49	0.25	1.74	11.03
M. punctifera	0.00	0.24	0.25	1.47	0.00	0.00	0.50	0.00
M. SMALL	2.19	0.00	0.00	0.00	0.00	0.75	1.00	0.49
M. tonsurata	0.97	0.48	0.25	1.47	0.00	2.00	0.50	1.47
M. torquata	0.24	0.24	0.00	0.98	0.24	0.50	0.50	0.25
M. transsylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.49	11.06	0.75	0.00	0.00	0.75	8.46	0.98
S. echinulata	5.11	9.86	8.21	0.98	0.00	7.23	9.45	1.23
S. petersenii	17.27	23.32	8.46	22.36	67.32	24.69	39.05	13.24
S. sphagnicola	29.44	0.48	67.66	3.93	23.17	39.40	1.00	1.23
S. spinosa	3.41	2.40	0.00	2.95	0.24	1.00	5.22	1.96
S. uvella	0.73	20.43	0.00	0.00	0.00	2.49	8.21	0.49
Chrysosphaerella spp	5.84	1.20	2.99	3.44	3.41	6.48	1.74	20.34
Paraphysomonas spp	0.73	0.48	0.00	0.25	0.00	0.00	0.25	0.25
Spiniferomonas spp	0.73	0.72	0.25	0.74	0.00	0.25	1.24	1.23

Appendix D (continued)

Muskoka-Haliburton (Tops)
Relative abundance data

	Gravenhurst	Green	Gullfeather	Haliburton	Hall's	Hamer Bay	Hammel Bay	Harp
Taxa								
Mallomonas acaroides f. muskokana	0.00	0.00	5.93	0.00	0.00	0.00	0.00	0.00
M. akrokomos	0.24	0.50	0.00	0.00	0.00	0.25	0.25	0.00
M. caudata	1.21	1.74	0.74	0.98	5.24	0.74	2.46	1.23
M. crassisquama	9.93	6.97	3.70	9.56	5.74	7.86	6.88	14.29
M. duerrschmidtiae	0.24	0.00	2.96	1.23	11.22	43.24	1.47	23.15
M. elongata	0.00	1.24	0.99	0.49	0.75	0.49	0.00	0.74
M. galeiformis	0.00	0.00	0.25	0.00	0.75	0.49	0.00	0.74
M. hamata	0.00	1.99	1.23	2.70	13.22	10.07	1.23	0.25
M. heterospina	0.48	0.00	0.00	0.00	0.25	0.00	0.74	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.49
M. lychenensis	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00
M. MEDIUM	0.24	0.75	0.49	0.49	0.25	0.25	0.00	2.96
M. pseudocoronata	0.97	1.99	1.23	2.45	11.22	9.09	1.72	34.24
M. punctifera	0.00	0.75	1.73	0.00	0.00	0.00	0.25	1.97
M. SMALL	0.73	1.24	1.23	0.49	0.25	0.98	0.25	0.25
M. tonsurata	1.45	0.00	1.23	1.47	0.75	0.98	0.98	1.72
M. torquata	0.24	1.99	1.23	0.25	0.75	0.49	0.25	0.74
M. transsylvanica	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00
Synura curtispina	1.21	4.73	0.49	2.21	0.25	0.49	0.98	0.00
S. echinulata	5.57	37.81	17.53	4.90	1.75	1.72	2.70	0.74
S. petersenii	69.49	24.38	12.10	48.04	27.18	7.86	72.24	5.17
S. sphagnicola	5.57	0.25	37.78	0.25	9.23	0.25	2.46	7.64
S. spinosa	1.45	4.23	0.99	5.64	2.74	1.47	1.47	1.72
S. uvella	0.00	4.48	2.22	16.18	4.24	0.49	0.74	0.00
Chrysosphaerella spp	0.73	3.73	5.93	0.98	0.75	11.30	2.46	1.23
Paraphysomonas spp	0.00	0.50	0.00	0.49	0.75	0.00	0.25	0.00
Spiniferomonas spp	0.24	0.75	0.25	1.23	2.74	0.49	0.25	0.74

	Heney	Kasha. S.	Kasha. N.	Kelly	Kennensis	Kushog North	Kushog South	Leech
Taxa								
Mallomonas acaroides f. muskokana	2.00	0.00	0.00	0.00	0.00	0.23	0.00	0.49
M. akrokomos	0.00	0.00	0.25	0.72	0.00	0.47	0.76	0.00
M. caudata	1.50	6.37	6.48	1.91	5.46	4.46	3.30	3.89
M. crassisquama	3.99	24.26	8.98	3.11	11.17	12.44	11.17	8.52
M. duerrschmidtiae	18.95	0.74	0.75	8.37	24.07	2.58	2.54	1.95
M. elongata	0.00	1.47	1.25	1.44	0.50	0.00	0.00	0.73
M. galeiformis	0.00	0.00	0.00	0.24	0.00	1.64	1.27	0.00
M. hamata	3.24	1.96	0.25	3.59	10.92	3.29	6.85	0.00
M. heterospina	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
M. lychenensis	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
M. MEDIUM	0.00	3.43	2.49	0.24	0.50	0.00	0.00	0.49
M. pseudocoronata	1.75	3.43	1.00	3.11	4.96	0.70	2.03	0.00
M. punctifera	1.75	0.49	0.50	0.00	0.00	0.47	0.00	0.00
M. SMALL	0.25	0.49	0.00	0.00	0.00	0.70	1.52	0.00
M. tonsurata	0.00	0.98	0.50	0.48	0.99	6.34	3.55	0.00
M. torquata	1.00	0.25	0.25	0.72	0.25	0.23	1.27	0.24
M. transsylvanica	0.25	0.00	0.00	0.00	0.00	0.47	0.00	0.00
Synura curtispina	0.00	9.56	8.73	0.00	0.25	0.70	0.76	0.00
S. echinulata	0.25	9.56	13.47	0.96	0.50	5.16	6.60	0.49
S. petersenii	1.50	14.71	43.89	53.83	22.58	19.01	14.72	63.26
S. sphagnicola	59.35	0.00	0.75	8.61	0.00	21.36	25.13	11.68
S. spinosa	0.50	1.72	2.99	7.89	6.70	6.81	8.38	5.35
S. uvella	0.00	19.12	6.73	2.39	8.44	3.99	2.03	1.46
Chrysosphaerella spp	3.49	0.49	0.25	1.91	1.49	7.04	6.60	0.49
Paraphysomonas spp	0.00	0.25	0.00	0.24	0.74	0.94	0.51	0.00
Spiniferomonas spp	0.25	0.49	0.50	0.24	0.50	0.70	0.51	0.24

Appendix D (continued)

Muskoka-Haliburton (Tops)
Relative abundance data

Taxa	Leonard	Little Clear	Little Kennensis	Little Redstone	Maple	McKay	Moose	Muskoka
Mallomonas acaroides f. muskokana	1.19	0.92	7.13	4.90	0.00	0.92	0.00	0.00
M. akrokomos	0.00	0.92	1.97	1.23	1.49	0.00	1.22	0.00
M. caudata	3.80	0.23	2.21	3.92	0.74	1.61	4.88	1.20
M. crassisquama	4.99	14.55	2.95	3.68	11.91	3.46	13.90	6.51
M. duerrschmidtiae	7.60	1.39	9.34	1.72	0.50	3.23	0.98	0.24
M. elongata	0.00	0.00	0.25	0.49	0.00	0.00	3.17	0.00
M. galeiformis	0.00	0.00	1.97	1.23	0.00	0.00	0.00	0.00
M. hamata	1.90	3.46	14.50	5.64	1.49	3.23	4.15	0.72
M. heterospina	0.24	1.39	0.49	0.98	0.25	0.23	1.22	0.00
M. lelymene	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
M. lychenensis	0.24	0.00	0.00	0.00	0.00	0.23	0.00	0.00
M. MEDIUM	0.00	0.23	0.25	0.25	0.50	0.23	0.73	0.00
M. pseudocoronata	0.48	0.92	1.97	1.47	1.24	0.69	2.68	0.48
M. punctifera	0.24	0.23	0.00	0.00	0.00	0.46	0.00	0.00
M. SMALL	0.24	0.23	1.23	0.98	0.99	0.23	1.22	0.00
M. tonsurata	0.00	0.23	2.21	1.47	0.25	1.38	1.46	0.96
M. torquata	0.24	0.69	1.23	1.23	0.99	0.46	0.73	0.24
M. transsylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.71	1.15	0.00	0.49	2.73	0.23	4.15	1.69
S. echinulata	4.75	3.23	3.69	7.11	41.94	1.61	8.78	5.30
S. petersenii	7.13	26.56	31.45	37.50	23.57	30.65	31.22	65.78
S. sphagnicola	63.42	0.23	6.63	12.99	0.99	43.09	0.49	11.81
S. spinosa	1.43	4.39	3.44	3.19	2.23	0.46	3.41	0.72
S. uvella	0.71	1.39	0.98	0.49	3.72	2.76	12.68	0.96
Chrysosphaerella spp	0.24	36.03	4.18	6.86	3.47	3.92	1.71	1.69
Paraphysomonas spp	0.24	0.92	0.25	1.23	0.50	0.00	0.24	1.69
Spiniferomonas spp	0.24	0.69	1.47	0.74	0.25	0.69	0.98	0.00

Taxa	Oblong	Plastic	Red Chalk E.	Red Chalk M.	Red Pine	Redstone	Roothog Island	Seagull Rock
Mallomonas acaroides f. muskokana	0.00	3.47	0.00	0.25	0.00	0.50	0.00	0.25
M. akrokomos	0.96	0.00	0.72	0.49	1.23	0.00	0.00	0.25
M. caudata	1.20	7.92	4.56	2.21	6.90	7.73	4.26	4.70
M. crassisquama	10.82	5.45	10.07	4.42	0.49	4.24	20.30	21.78
M. duerrschmidtiae	0.96	12.62	4.56	3.69	4.19	4.49	16.79	23.27
M. elongata	0.72	0.00	0.72	0.00	0.25	1.75	0.25	0.25
M. galeiformis	0.00	0.00	0.48	0.25	0.25	0.25	1.00	1.24
M. hamata	1.92	5.45	6.24	3.69	7.64	9.73	5.26	4.21
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lychenensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
M. MEDIUM	0.00	0.00	0.48	0.25	0.00	0.25	0.00	2.48
M. pseudocoronata	3.61	1.98	6.00	0.25	1.23	1.75	4.26	7.67
M. punctifera	0.72	0.74	0.48	1.97	0.00	0.00	0.50	0.99
M. SMALL	0.48	0.74	0.96	0.00	0.00	0.75	0.50	0.74
M. tonsurata	0.24	0.50	0.96	0.98	1.48	0.50	4.51	2.48
M. torquata	0.48	2.97	0.24	0.49	0.00	0.75	1.00	1.49
M. transsylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Synura curtispina	4.81	0.00	0.00	0.25	0.00	0.00	0.25	1.24
S. echinulata	4.09	5.45	1.44	2.70	1.23	1.25	2.01	2.72
S. petersenii	51.92	6.93	24.94	15.23	50.74	32.17	18.05	9.90
S. sphagnicola	0.00	36.88	4.56	31.20	1.48	2.74	5.76	4.95
S. spinosa	8.41	0.74	17.75	5.90	17.98	17.71	2.76	1.24
S. uvella	7.21	0.00	10.55	0.98	1.48	6.73	5.51	2.72
Chrysosphaerella spp	0.72	7.18	3.36	23.59	2.71	5.49	6.52	2.72
Paraphysomonas spp	0.00	0.25	0.48	0.74	0.00	0.25	0.25	0.74
Spiniferomonas spp	0.72	0.50	0.48	0.49	0.74	1.00	0.25	0.99

Appendix D (continued)

Muskoka-Haliburton (Tops)
Relative abundance data

	Solitaire	Soyer's	St. Nora	Walker	Young
Taxa					
Mallomonas acaroides f. muskokana	0.00	0.00	0.25	0.99	0.00
M. akrokomos	1.60	0.00	0.25	0.50	0.00
M. caudata	13.24	2.74	5.65	1.24	8.18
M. crassisquama	14.84	2.99	8.85	2.73	15.89
M. duerrschmidtiae	10.05	0.25	5.41	0.50	2.80
M. elongata	0.68	0.75	0.98	0.50	0.70
M. galeiformis	0.00	0.00	1.72	0.00	0.00
M. hamata	10.73	0.25	4.67	1.49	3.74
M. heterospina	2.05	0.25	0.25	0.00	0.00
M. lelymene	0.23	0.00	0.00	0.00	1.87
M. lychenensis	0.00	0.00	0.00	0.00	1.17
M. MEDIUM	0.68	0.00	0.25	0.00	0.23
M. pseudocoronata	3.20	0.75	1.23	0.74	13.55
M. punctifera	0.23	0.50	0.00	0.00	1.64
M. SMALL	0.46	0.50	1.72	0.25	0.23
M. tonsurata	0.46	0.50	4.18	0.25	0.47
M. torquata	0.23	0.75	0.74	0.25	0.93
M. transylvanica	0.23	0.00	0.00	0.00	0.93
Synura curtispina	0.91	1.75	0.00	0.25	13.79
S. echinulata	0.68	50.87	1.72	14.39	27.34
S. petersenii	26.71	17.21	25.55	47.64	0.47
S. sphagnicola	0.00	0.25	28.01	6.20	0.00
S. spinosa	9.36	7.23	3.19	3.97	4.91
S. uvella	2.05	9.48	1.47	2.73	0.00
Chrysosphaerella spp	0.00	2.74	2.46	14.39	0.23
Paraphysomonas spp	0.00	0.00	0.00	0.25	0.00
Spiniferomonas spp	1.37	0.25	1.23	0.74	0.93

Appendix E: Relative abundance species data from 48 pre-industrial sediment samples

Muskoka-Haliburton (Bottoms)
Relative abundance data

	12 Mile	Bass	Basshaunt	Bigwind	Blue Chalk	Boshkung	Buck	Canning
Taxa								
Mallomonas acaroides f. muskokana	0.00	0.99	0.00	0.92	0.00	0.00	0.00	0.00
M. akrokomos	0.00	0.00	0.00	0.92	0.00	0.00	0.00	0.32
M. caudata	4.98	0.99	3.47	3.98	2.39	2.99	2.99	4.21
M. crassisquama	10.96	11.39	19.11	20.18	21.51	15.95	12.29	22.33
M. duerrschmidtiae	40.86	41.58	34.24	24.46	50.60	52.49	73.09	13.92
M. elongata	0.33	0.00	0.99	1.22	0.00	1.00	0.66	0.00
M. galeiformis	0.66	0.00	0.25	0.00	0.00	0.00	0.00	0.00
M. hamata	1.99	0.00	2.23	4.89	0.40	2.99	0.33	0.32
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.00
M. lychenensis	1.00	2.97	25.81	1.53	2.39	0.66	3.99	2.27
M. MEDIUM	1.66	0.00	0.25	0.61	0.40	2.33	0.00	1.94
M. pseudocoronata	20.93	36.63	1.49	14.98	10.36	8.31	3.32	33.01
M. punctifera	2.33	0.00	0.25	3.98	0.00	0.33	0.00	0.00
M. SMALL	0.33	0.00	0.99	0.00	0.40	0.66	0.00	0.00
M. tonsurata	2.99	0.00	1.74	1.83	5.58	2.66	0.33	2.59
M. torquata	0.33	0.00	0.25	0.61	0.40	1.00	0.00	0.32
M. transylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.32
S. echinulata	1.00	0.99	0.74	0.61	0.00	1.00	0.00	9.39
S. petersenii	6.64	0.00	3.72	8.56	0.40	5.65	0.00	6.15
S. sphagnicola	1.00	0.99	0.25	0.31	0.00	0.33	0.00	0.32
S. spinosa	0.66	0.00	0.50	0.61	0.00	0.00	0.00	0.32
S. uvella	0.00	1.98	3.47	7.95	2.79	0.00	2.99	1.94
Chrysosphaerella spp	0.33	0.00	0.00	0.92	0.80	0.33	0.00	0.32
Paraphysomonas spp	0.00	0.00	0.00	0.31	0.00	0.33	0.00	0.00
Spiniferomonas spp	0.66	1.49	0.25	0.61	0.00	0.33	0.00	0.00

	Chub	Clear	Crosson	Dickie	Eagle	Gravenhurst	Green	Gullfeather
Taxa								
Mallomonas acaroides f. muskokana	0.00	0.00	1.33	2.68	0.00	0.33	0.00	0.97
M. akrokomos	0.33	0.00	0.00	0.00	0.00	0.98	0.65	0.24
M. caudata	1.32	0.00	1.66	1.79	1.66	1.97	3.90	0.73
M. crassisquama	16.23	0.84	10.63	5.06	11.59	14.43	13.31	4.13
M. duerrschmidtiae	21.19	11.76	7.97	36.61	11.92	9.84	6.17	14.32
M. elongata	0.99	0.00	0.00	0.00	0.33	0.33	0.32	0.49
M. galeiformis	0.66	0.00	0.66	1.19	0.00	2.30	0.00	0.97
M. hamata	1.99	1.68	1.33	0.89	2.65	6.89	5.19	2.67
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lychenensis	0.66	61.34	2.66	0.89	2.32	5.90	7.79	2.43
M. MEDIUM	0.00	0.00	0.00	0.00	0.99	0.33	2.27	0.49
M. pseudocoronata	7.95	9.24	6.31	0.89	33.77	14.43	5.19	3.40
M. punctifera	2.98	0.00	0.33	1.19	0.33	1.31	0.32	1.21
M. SMALL	0.99	1.68	0.66	0.60	0.99	0.00	1.30	0.49
M. tonsurata	4.64	0.00	2.99	6.25	3.64	9.51	5.52	7.04
M. torquata	2.32	0.00	2.99	0.00	0.00	1.97	0.32	2.91
M. transylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.66	0.00	0.00	0.00	0.00	0.33	0.65	0.00
S. echinulata	6.95	3.36	40.20	29.76	3.64	2.30	4.87	3.16
S. petersenii	12.58	0.84	8.97	2.38	16.89	10.49	25.97	3.16
S. sphagnicola	9.60	0.84	3.99	5.06	0.66	4.26	1.30	48.54
S. spinosa	2.65	0.00	0.00	0.00	0.99	0.33	0.65	0.00
S. uvella	2.65	1.68	3.99	4.17	5.30	3.28	2.27	2.18
Chrysosphaerella spp	1.99	0.00	1.66	0.30	1.66	8.52	9.09	0.24
Paraphysomonas spp	0.66	4.20	0.33	0.00	0.33	0.00	0.97	0.00
Spiniferomonas spp	0.00	2.52	1.33	0.30	0.33	0.00	1.95	0.24

Appendix E (continued)

Muskoka-Haliburton (Bottoms)
Relative abundance data

Taxa	Haliburton	Hall's	Hamer Bay	Hammel Bay	Harp	Kasha, S.	Kasha, N.	Kelly
Mallomonas acaroides f. muskokana	0.00	0.00	0.00	0.33	0.74	0.00	0.00	0.25
M. akrokomos	0.00	1.66	0.33	1.64	0.00	0.33	0.99	0.75
M. caudata	5.96	2.66	0.98	4.59	2.98	5.32	3.31	1.25
M. crassisquama	10.93	18.27	6.21	8.20	13.40	12.29	20.20	14.21
M. duerrschmidtiae	9.93	51.50	73.53	23.61	41.44	12.29	5.63	59.10
M. elongata	0.66	2.33	0.00	0.00	0.00	0.66	0.66	0.75
M. galeiformis	0.33	0.33	0.33	0.33	2.98	0.00	0.33	2.24
M. hamata	0.66	6.31	4.25	2.95	7.69	5.65	1.66	2.49
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00
M. lychenensis	4.30	0.33	5.23	6.89	1.74	2.33	1.32	0.50
M. MEDIUM	4.64	0.33	0.00	0.98	0.50	5.98	1.66	0.25
M. pseudocoronata	21.19	4.98	5.88	3.61	5.71	15.61	16.23	3.24
M. punctifera	1.32	0.00	0.65	0.33	7.94	0.00	0.33	2.00
M. SMALL	0.66	1.66	0.33	0.33	0.50	0.66	0.66	0.25
M. tonsurata	1.99	1.99	1.63	1.31	8.44	4.65	4.64	3.99
M. torquata	0.66	0.33	0.00	0.98	0.74	1.00	1.99	0.50
M. transylvanica	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.25
S. echinulata	12.58	0.33	0.33	13.11	0.00	4.65	19.21	0.00
S. petersenii	7.62	2.33	0.00	20.98	1.99	23.59	13.58	2.24
S. sphagnicola	0.00	1.33	0.00	6.89	0.00	0.66	1.32	0.00
S. spinosa	2.32	0.66	0.00	0.00	1.49	0.33	1.99	1.00
S. uvella	13.58	0.66	0.00	1.31	0.00	0.33	2.65	3.99
Chrysosphaerella spp	0.00	1.00	0.33	1.31	0.25	1.99	0.33	0.00
Paraphysomonas spp	0.00	1.00	0.00	0.00	0.50	0.66	0.99	0.75
Spiniferomonas spp	0.33	0.00	0.00	0.33	0.25	0.66	0.33	0.00

Taxa	Kennensis	Kushog, N.	Kushog, S.	Leech	Leonard	Little Clear	Little Kennensis	Little Redstone
Mallomonas acaroides f. muskokana	0.00	5.13	1.00	0.98	3.96	1.72	0.00	1.32
M. akrokomos	0.33	2.24	1.00	0.65	0.00	0.49	0.33	0.99
M. caudata	3.00	1.92	1.66	1.96	2.48	2.46	2.98	2.63
M. crassisquama	9.33	6.73	18.27	10.46	13.12	48.03	9.93	17.11
M. duerrschmidtiae	37.67	33.33	18.94	7.52	58.17	12.81	19.87	18.09
M. elongata	1.33	0.64	0.00	0.98	0.25	2.46	0.00	0.00
M. galeiformis	0.67	0.96	1.66	0.65	0.99	0.00	1.32	1.32
M. hamata	6.00	4.17	1.99	3.27	0.74	2.46	6.95	2.30
M. heterospina	0.00	0.00	0.66	0.00	0.00	0.25	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.98	0.25	0.49	0.00	0.00
M. lychenensis	0.67	0.64	0.00	0.98	7.43	0.25	0.33	0.33
M. MEDIUM	0.33	1.28	0.66	0.98	1.98	1.23	0.00	0.66
M. pseudocoronata	3.33	11.86	8.31	1.63	1.98	1.23	1.99	8.55
M. punctifera	2.33	5.45	1.00	0.33	0.99	2.22	3.64	3.62
M. SMALL	0.33	0.32	1.99	1.63	0.00	0.25	0.66	1.32
M. tonsurata	6.33	7.69	4.65	1.31	1.73	0.25	3.31	4.28
M. torquata	0.33	1.28	1.66	1.31	0.00	0.00	1.32	0.33
M. transylvanica	0.00	0.00	0.00	0.00	0.25	0.00	0.33	0.33
Synura curtispina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. echinulata	1.33	0.32	1.00	11.76	0.25	0.74	2.32	4.61
S. petersenii	6.67	9.94	13.95	10.78	1.73	6.65	9.60	18.75
S. sphagnicola	3.00	0.00	13.29	30.07	0.25	0.00	21.19	1.32
S. spinosa	4.33	0.00	1.00	1.96	0.00	7.14	1.66	0.66
S. uvella	9.67	0.00	3.99	2.94	3.22	5.67	6.29	0.99
Chrysosphaerella spp	2.00	4.49	2.66	6.21	0.25	2.46	4.30	8.88
Paraphysomonas spp	1.00	0.32	0.33	0.00	0.00	0.49	0.66	0.00
Spiniferomonas spp	0.00	1.28	0.33	0.65	0.00	0.25	0.99	1.64

Appendix E (continued)

Muskoka-Haliburton (Bottoms)
Relative abundance data

Taxa	Maple	McKay	Moose	Muskoka	Oblong	Red Chalk E.	Red Chalk M.	Red Pine
Mallomonas acaroides f. muskokana	0.00	3.57	0.00	0.33	0.00	0.00	0.00	0.00
M. akrokomos	1.00	0.32	0.99	0.65	0.33	0.00	2.44	1.64
M. caudata	2.33	0.97	3.97	1.30	4.90	2.88	1.47	0.66
M. crassisquama	25.25	4.55	14.57	18.24	11.76	29.81	9.78	7.89
M. duerrschmidtiae	16.28	12.99	12.58	14.01	21.24	30.77	14.18	24.01
M. elongata	0.00	0.00	0.99	0.00	0.65	0.00	0.00	0.33
M. galeiformis	0.66	0.00	0.00	2.28	0.33	0.00	1.47	2.30
M. hamata	0.66	2.60	2.32	3.58	2.29	0.00	6.85	9.54
M. heterospina	0.33	0.00	0.00	0.00	0.00	0.00	0.24	0.00
M. lelymene	0.00	0.32	0.00	0.33	0.00	0.00	0.00	0.00
M. lychenensis	6.31	0.32	6.62	4.23	2.29	0.96	0.73	0.00
M. MEDIUM	0.33	0.00	0.33	0.65	1.63	0.00	0.49	0.00
M. pseudocoronata	9.97	1.30	25.83	7.17	13.07	29.81	0.73	7.89
M. punctifera	0.66	2.27	0.33	0.33	0.33	0.00	9.29	0.66
M. SMALL	1.00	0.32	0.66	0.65	0.65	0.00	0.00	1.64
M. tonsurata	4.98	2.60	4.97	4.89	2.94	0.96	11.00	5.92
M. torquata	3.65	2.27	0.66	2.28	0.00	0.00	0.73	0.33
M. transsylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00
S. echinulata	6.64	6.17	2.65	2.28	6.54	0.00	1.71	2.30
S. petersenii	12.96	17.53	10.60	12.05	9.48	0.00	11.98	7.89
S. sphagnicola	0.00	20.78	0.66	6.51	0.00	0.00	6.11	11.84
S. spinosa	2.33	0.32	0.33	0.33	2.61	0.96	1.71	2.30
S. uvella	1.66	2.60	6.62	3.26	13.73	1.92	3.42	2.96
Chrysosphaerella spp	0.66	17.86	3.31	12.70	3.59	0.96	13.45	7.57
Paraphysomonas spp	1.33	0.32	0.33	0.98	0.33	0.00	1.71	0.33
Spiniferomonas spp	1.00	0.00	0.33	0.98	0.33	0.96	0.49	1.97

Taxa	Redstone	Roothog Island	Seagull Rock	Solitaire	Soyer's	St. Nora	Walker	Young
Mallomonas acaroides f. muskokana	0.00	0.00	0.00	1.00	0.00	0.99	4.92	0.63
M. akrokomos	0.00	0.00	0.00	0.00	1.33	0.00	0.00	0.32
M. caudata	21.00	3.23	0.42	3.00	1.99	3.96	11.80	2.22
M. crassisquama	35.00	17.34	15.55	23.00	8.97	23.76	16.72	13.33
M. duerrschmidtiae	0.00	49.19	56.72	26.00	6.31	24.75	6.89	25.40
M. elongata	0.00	0.40	0.00	0.00	0.00	0.00	1.64	1.27
M. galeiformis	0.00	2.42	0.42	0.00	1.00	0.00	0.66	0.63
M. hamata	0.00	1.21	2.52	3.00	1.33	0.00	1.31	1.27
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00
M. lychenensis	0.00	0.81	0.84	5.00	1.99	0.99	1.97	6.03
M. MEDIUM	0.00	0.00	2.10	0.00	2.99	0.00	0.98	0.95
M. pseudocoronata	21.00	14.11	11.34	5.00	7.64	42.57	13.77	31.43
M. punctifera	0.00	2.02	0.84	0.00	0.00	0.00	1.31	4.44
M. SMALL	1.00	1.21	0.42	0.00	1.99	0.00	0.66	0.32
M. tonsurata	1.00	3.23	1.26	0.00	4.32	1.98	5.57	3.17
M. torquata	2.00	0.81	1.26	0.00	1.33	0.99	0.33	0.00
M. transsylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.90
Synura curtispina	0.00	0.00	0.00	0.00	0.00	0.00	0.33	1.59
S. echinulata	0.00	0.40	0.00	0.00	9.63	0.00	2.30	0.32
S. petersenii	0.00	1.61	0.84	0.00	36.21	0.00	3.93	0.32
S. sphagnicola	1.00	0.00	1.68	0.00	5.32	0.00	0.66	0.00
S. spinosa	0.00	0.00	0.84	2.00	0.33	0.00	0.98	0.00
S. uvella	2.00	0.40	0.00	29.00	1.33	0.00	15.74	0.95
Chrysosphaerella spp	2.00	1.61	2.52	0.00	4.98	0.00	5.90	3.17
Paraphysomonas spp	3.00	0.00	0.42	1.00	0.33	0.00	0.98	0.32
Spiniferomonas spp	0.00	0.00	0.00	0.00	0.66	0.00	0.66	0.00

Appendix F: Relative abundance species data from top and bottom triplicate samples

Muskoka-Haliburton (Triplicates)
Relative abundance data

	Bass-t1	Bass-t2	Bass-t3	Bass-b1	Bass-b2	Bass-b3
Taxa						
Mallomonas acaroides f. muskokana	0.61	0.66	2.30	0.99	0.00	0.00
M. akrokomos	0.61	0.33	0.33	0.00	0.00	0.33
M. caudata	0.92	1.66	1.97	0.99	1.31	0.33
M. crassisquama	2.75	2.98	1.64	11.39	15.03	17.55
M. duerrschmidtiae	0.92	0.66	0.98	41.58	44.77	39.40
M. elongata	0.00	0.00	0.00	0.00	0.00	0.33
M. galeiformis	0.00	0.33	0.33	0.00	0.00	0.00
M. hamata	0.31	0.66	0.66	0.00	0.00	0.99
M. heterospina	0.31	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.31	0.00	0.00	0.00	0.00	0.66
M. lychenensis	0.00	0.00	0.00	2.97	2.94	3.31
M. MEDIUM	0.00	0.00	0.33	0.00	0.33	0.00
M. pseudocoronata	1.83	0.99	1.31	36.63	29.41	29.80
M. punctifera	0.00	0.33	0.00	0.00	0.00	0.00
M. SMALL	2.14	0.66	1.64	0.00	0.00	0.66
M. tonsurata	1.83	1.32	0.98	0.00	0.33	0.66
M. torquata	0.00	0.33	0.98	0.00	0.98	0.66
M. trannsylvanica	0.00	0.00	0.00	0.00	0.33	0.00
Synura curtispina	0.61	0.99	0.66	0.00	0.33	0.00
S. echinulata	6.12	7.95	6.89	0.99	1.63	1.66
S. petersenii	18.04	16.56	14.43	0.00	0.33	0.66
S. sphagnicola	37.00	33.44	37.38	0.99	0.33	0.33
S. spinosa	2.75	4.64	2.30	0.00	0.00	0.33
S. uvella	1.83	2.98	1.97	1.98	0.98	0.66
Chrysosphaerella spp	19.57	22.19	22.62	0.00	0.00	0.33
Paraphysomonas spp	0.61	0.33	0.00	0.00	0.33	0.99
Spiniferomonas spp	0.92	0.00	0.33	1.49	0.65	0.33

	Crosson-t1	Crosson-t2	Crosson-t3	Crosson-b1	Crosson-b2	Crosson-b3
Taxa						
Mallomonas acaroides f. muskokana	0.63	0.97	0.98	2.62	3.03	1.33
M. akrokomos	0.00	0.00	0.00	1.17	0.30	0.00
M. caudata	2.19	1.29	0.98	2.62	4.85	1.66
M. crassisquama	0.00	0.00	0.73	12.83	7.27	10.63
M. duerrschmidtiae	1.57	3.24	1.71	14.29	14.85	7.97
M. elongata	0.00	0.00	0.00	0.00	0.00	0.00
M. galeiformis	0.00	0.00	0.00	0.87	1.21	0.66
M. hamata	0.94	0.00	0.73	2.62	1.52	1.33
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00
M. lychenensis	0.00	0.00	0.00	0.87	0.30	1.99
M. MEDIUM	0.00	0.00	0.00	0.00	0.91	0.00
M. pseudocoronata	0.00	0.65	0.49	4.66	4.24	6.31
M. punctifera	0.00	0.00	0.00	0.00	0.00	0.00
M. SMALL	0.31	0.00	0.00	0.58	0.30	0.66
M. tonsurata	0.31	0.32	0.00	5.25	3.64	2.99
M. torquata	0.94	0.97	0.24	2.62	9.39	2.99
M. trannsylvanica	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.00	0.00	0.00	0.58	0.00	0.00
S. echinulata	0.63	0.65	0.00	22.45	3.64	40.20
S. petersenii	76.49	66.34	67.32	12.54	20.00	8.97
S. sphagnicola	13.79	23.30	23.17	5.25	17.27	3.99
S. spinosa	0.31	0.65	0.24	0.00	0.00	0.00
S. uvella	0.00	0.00	0.00	3.79	3.94	3.99
Chrysosphaerella spp	1.88	0.97	3.41	2.04	1.21	1.66
Paraphysomonas spp	0.00	0.32	0.00	0.00	1.21	0.33
Spiniferomonas spp	0.00	0.00	0.00	0.29	0.30	1.33

Appendix F (continued)

Muskoka-Haliburton (Triplicates)
Relative abundance data

	Dickie-t1	Dickie-t2	Dickie-t3	Dickie-b1	Dickie-b2	Dickie-b3
Taxa						
Mallomonas acaroides f. muskokana	2.74	2.48	2.80	2.68	2.52	2.24
M. akrokomos	0.75	0.00	0.00	0.00	0.63	0.00
M. caudata	2.24	3.42	3.12	1.79	1.89	0.64
M. crassisquama	2.00	3.42	2.80	5.06	5.68	2.56
M. duerrschmidtiae	4.24	6.52	2.18	36.61	29.65	30.67
M. elongata	0.00	0.62	0.93	0.00	0.95	0.00
M. galeiformis	0.50	1.24	0.62	1.19	0.32	0.64
M. hamata	1.25	1.24	0.93	0.89	3.47	0.96
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.00
M. lelymene	0.00	0.00	0.31	0.00	1.58	0.00
M. lychenensis	0.25	0.00	0.31	0.60	1.89	0.32
M. MEDIUM	0.25	0.00	0.00	0.00	0.00	0.00
M. pseudocoronata	0.25	0.93	0.00	0.89	0.95	0.64
M. punctifera	0.00	0.31	0.00	0.00	0.32	0.00
M. SMALL	0.75	0.31	0.62	0.60	0.95	0.32
M. tonsurata	2.00	3.11	3.12	6.25	6.31	6.71
M. torquata	0.50	1.24	1.56	0.00	1.26	0.96
M. transsylvanica	0.00	0.00	0.00	0.00	0.00	0.00
Synura curtispina	0.75	0.00	0.00	0.00	0.00	0.00
S. echinulata	7.23	7.14	8.72	29.76	1.89	36.10
S. petersenii	24.69	21.74	27.10	2.38	10.09	4.79
S. sphagnicola	39.40	38.20	33.33	5.06	23.03	4.15
S. spinosa	1.00	2.80	2.49	0.00	1.58	0.64
S. uvella	2.49	2.17	2.49	4.17	1.58	4.15
Chrysosphaerella spp	6.48	2.80	5.92	0.30	2.21	1.60
Paraphysomonas spp	0.00	0.31	0.31	0.00	0.32	0.64
Spiniferomonas spp	0.25	0.00	0.00	0.30	0.32	0.64

	Halib.-t1	Halib.-t2	Halib.-t3	Halib.-b1	Halib.-b2	Halib.-b3
Taxa						
Mallomonas acaroides f. muskokana	0.00	0.00	0.00	0.00	0.00	0.00
M. akrokomos	0.00	0.00	0.00	0.97	0.00	0.98
M. caudata	1.95	0.98	1.66	2.58	6.16	4.25
M. crassisquama	6.51	9.56	12.62	9.03	11.30	9.80
M. duerrschmidtiae	0.65	1.23	0.66	13.23	6.85	15.36
M. elongata	1.63	0.49	0.66	0.32	0.68	0.33
M. galeiformis	0.00	0.00	0.00	0.00	0.34	0.00
M. hamata	1.63	2.70	1.33	0.65	0.68	0.98
M. heterospina	0.00	0.00	0.00	0.00	0.00	0.33
M. lelymene	0.00	0.00	0.00	0.00	0.00	0.00
M. lychenensis	0.00	0.00	0.00	2.58	4.45	3.92
M. MEDIUM	0.65	0.49	0.66	5.16	4.79	4.90
M. pseudocoronata	9.12	2.45	9.30	17.74	21.92	18.95
M. punctifera	0.33	0.00	0.00	0.32	1.37	1.96
M. SMALL	0.65	0.49	0.33	0.32	0.68	0.65
M. tonsurata	0.33	1.47	0.33	4.19	2.05	2.29
M. torquata	1.30	0.25	1.00	0.32	0.68	0.33
M. transsylvanica	0.00	0.00	0.00	0.32	0.34	0.00
Synura curtispina	0.98	2.21	0.66	1.29	0.00	0.00
S. echinulata	6.51	4.90	4.65	7.74	13.01	5.56
S. petersenii	42.67	48.04	41.20	10.97	7.88	8.50
S. sphagnicola	0.00	0.25	0.00	0.32	0.00	0.65
S. spinosa	8.47	5.64	4.98	4.52	2.40	0.98
S. uvella	14.98	16.18	18.27	12.90	14.04	13.40
Chrysosphaerella spp	1.30	0.98	0.66	3.23	0.00	3.27
Paraphysomonas spp	0.00	0.49	1.00	0.97	0.00	1.63
Spiniferomonas spp	0.33	1.23	0.00	0.00	0.34	0.33

Appendix F (continued)

Muskoka-Haliburton (Triplicates)
Relative abundance data

	L. Clear-t1	L. Clear-t2	L. Clear-t3	L. Clear-b1	L. Clear-b2	L. Clear-b3
Taxa						
Mallomonas acaroides f. muskokana	0.00	0.92	0.00	1.57	1.72	3.96
M. akrokomos	1.62	0.92	0.00	1.25	0.49	2.64
M. caudata	1.62	0.23	2.92	0.94	2.46	1.98
M. crassisquama	18.51	14.55	17.86	34.17	48.03	36.96
M. duerrschmidtiae	0.97	1.39	0.97	9.40	12.81	9.24
M. elongata	0.32	0.00	0.00	1.25	2.46	1.65
M. galeiformis	0.00	0.00	0.00	0.00	0.00	0.00
M. hamata	1.62	3.46	3.57	2.82	2.46	3.96
M. heterospina	1.62	1.39	0.32	0.63	0.25	0.66
M. lelymene	0.00	0.00	0.00	0.31	0.49	0.00
M. lychenensis	0.00	0.00	0.00	0.31	0.25	0.00
M. MEDIUM	0.32	0.23	0.32	1.57	1.23	0.66
M. pseudocoronata	0.00	0.92	0.00	1.57	1.23	2.64
M. punctifera	0.00	0.23	0.32	1.25	1.23	1.32
M. SMALL	0.00	0.23	0.00	2.19	0.25	0.33
M. tonsurata	0.00	0.23	0.00	0.31	0.25	0.66
M. torquata	0.32	0.69	0.32	0.31	0.00	0.00
M. trannsylvanica	0.32	0.00	0.00	0.63	0.00	0.00
Synura curtispina	0.97	1.15	2.27	0.00	0.00	0.00
S. echinulata	3.90	3.23	2.92	0.00	0.74	0.00
S. petersenii	21.10	26.56	24.68	10.34	6.65	13.53
S. sphagnicola	0.00	0.23	0.32	0.31	0.00	1.32
S. spinosa	12.99	4.39	9.09	8.46	7.14	4.95
S. uvella	1.62	1.39	2.27	6.27	5.67	1.98
Chrysosphaerella spp	31.17	36.03	29.87	11.60	2.46	8.91
Paraphysomonas spp	0.65	0.92	0.32	0.31	0.49	0.66
Spiniferomonas spp	0.32	0.69	1.62	0.31	0.25	0.99