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Trends and drivers of water clarity in shallow, prairie lakes of southern Alberta

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Trends and Drivers of Water Clarity in Shallow, Prairie Lakes of Southern Alberta

by

Heather Marie Maheux

A THESIS

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Abstract

This research examined water clarity in shallow, prairie lakes of southern Alberta. A combination of water column analyses from 20 lakes and paleolimnological analyses from ten of them were used to examine how water clarity has changed since 1850 and to identify possible explanations for the observed changes. Pigment data from sediment cores showed the lakes experienced accelerated eutrophication since 1850, but that the onset was not synchronous across lakes. The lakes showed evidence that regime shifts between clear and turbid lake regimes since 1850 were possible. Evidence was based on paleolimnological analyses using pigment data and additional sediment core proxies (e.g. fossils, isotopes). Water quality data from 20 lakes did not provide additional support for the existence of alternate regimes based on multimodal distribution between regimes or dual relationships between nutrients and water clarity. Salinity and major ion composition may help explain why some lakes did not provide additional support for the existence of alternate clear and turbid regimes. In most lakes, turbidity was dominated by inorganic matter, rather than phytoplankton, and this was more prevalent in the more saline lakes. High proportions of heterocystous cyanobacteria from 4 of the 20 shallow lakes provided some evidence for nitrogen limitation in the lakes. It is possible that additional lakes were also nutrient limited. As a result, models that use nutrient-chlorophyll relationships developed in non-saline lakes do not accurately capture turbidity dynamics in the saline, shallow lakes on southern Alberta's prairie.

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List of Abbreviations

Chl <i>a</i>	Chlorophyll <i>a</i>
C/N	Carbon : nitrogen ratio
$\delta^{13}\text{C}$	Carbon stable isotope ratio
GA	Great Acceleration
NTU	Nephelometric turbidity units
R	R language and software environment
SRP	Soluble reactive phosphorus
TC	Total carbon
TDS	Total dissolved solids
TN	Total nitrogen
TP	Total phosphorus
TSS	Total suspended solids

CHAPTER ONE: INTRODUCTION

Shallow lakes are often valued for agricultural irrigation, watering livestock and recreational opportunities. Less obvious services that these ecosystems provide are clean drinking water and critical habitat for migratory waterfowl and other wildlife. Shallow lakes are also important sites for nutrient cycling including processes such as carbon storage through biomass accumulation, nitrogen fixation and denitrification. Water clarity impacts the structure and function of shallow lakes. Clear lakes with light penetration to the sediments can support growth of macrophytes and benthic algae whereas turbid lakes are less likely to support benthic primary production due to light limitation (Scheffer, 1998).

Eutrophication in lakes has been generally well studied (e.g. Schindler, 2006). Still, it can be difficult to identify the specific drivers of eutrophication in individual lakes because there are many factors that influence phytoplankton biomass accumulation including nutrient concentrations, temperature, water chemistry and foodweb structure. Much of the eutrophication research has been done using deeper, stratified lakes. Shallow lakes, defined here as polymictic, permanent, lentic inland water bodies (Davis *et al.* 2010), differ because the entire water column continually mixes. This promotes sediment resuspension and nutrient recycling. Shallow depths also often enable light penetration to the sediments, making it possible for macrophytes and benthic algae to colonize sediments throughout the entire lake (Scheffer, 1998).

Small and shallow water bodies are abundant and ecologically important in Canada's agricultural prairies. The prairie region of Canada and the northern United

States is covered with hundreds of thousands to ten million pothole lakes and wetlands (Covich et al., 1997; Last and Ginn, 2005). Small lakes are important reservoirs of biodiversity within agricultural landscapes (Sondergaard et al., 2005), such as the Canadian prairies. Lakes and ponds in southern Alberta provide habitat to numerous species including migratory waterfowl and species at risk such as the northern leopard frog.

The goal of my research was to explore internal and external drivers of water clarity in shallow lakes on southern Alberta's prairie. I asked three specific questions about these lakes:

1. Is there evidence of a *Great Acceleration* (GA) in eutrophication circa 1945?
2. Do they exist under alternate clear and turbid regimes and do they show shifts between regimes over time?
3. Does salinity (composition and concentration) affect turbidity and, therefore, how alternate regime models for shallow lakes can be applied in southern Alberta?

These questions are addressed in chapters two to four. Each "data" chapter was written with publication in mind and, therefore, there is overlap between the current chapter and the introduction sections of individual data chapters.

Study Area

The primary focus of this study was 20 shallow lakes found in the mixedgrass ecoregion of southern Alberta's prairie (Strong, 1992). All 20 lakes are located within a 125 km radius of the town of Strathmore (Fig. 1.1), an agricultural area dominated by dark brown

or black Chernozemic soil. The region was grazed by bison (*Bison bison bison*) historically and, since European settlement in the mid-late 19th century, converted to agriculture. Wheat, barley and canola have been the primary crops in the area for at least the past 50 years while cattle ranching and pork production have been the primary livestock operations over the same time period (Statistics Canada, 1966-2006). Lakes in the area cover a wide range of salinities, from fresh to highly saline.

Great Acceleration

Human population growth, coupled with increased industrial activity, has had unprecedented influence on the world's ecosystems since the industrial revolution and, especially, since the Second World War (Crutzen, 2002). The global human population has grown by more than 2.7 fold (UN, 2011) since 1950 and exponential changes associated with industrial activity since 1945, such as increases in CO₂ emissions, water use and fertilizer consumption, have led some to call this period the Great Acceleration (GA) (Steffen *et al.*, 2007). Industrial change has led to significant environmental challenges. In particular, human activity is reaching or has surpassed the boundaries of what the planet can withstand in terms of climate change, biodiversity loss and changes in nutrient cycling (Rockström, *et al.*, 2009).

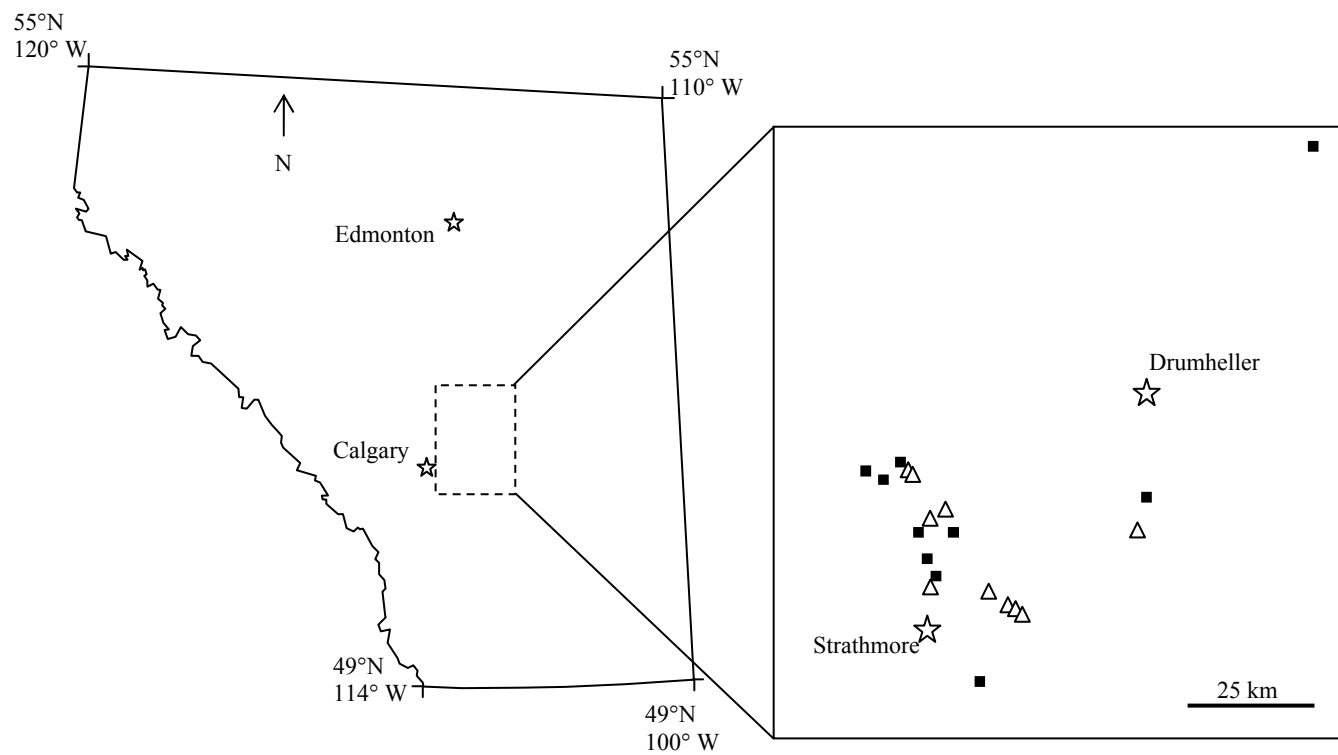


Figure 1.1. Study area within the mixed grass ecoregion of southern Alberta. Water samples were taken from 20 shallow lakes (black squares and open triangles). Sediment cores were taken from 10 of these lakes (open triangles).

Meeting the ever-increasing global demand for food, while minimizing environmental impacts, is a serious challenge (Foley et al., 2011, Townsend and Porder, 2012). Synthetic fertilizers are applied to nutrient-depleted soils to support high intensity agriculture and the rate of fertilizer consumption has increased steadily since the mid-1900s (Steffen et al., 2007). The UN Food and Agriculture Organization estimates that total fertilizer consumption, globally, more than quadrupled from 31 000 000 tonnes in 1961 to 141 000 000 tonnes in 2002 and that total meat production quadrupled between 1961 and 2010 (UN FAOStat, 2012a). Fertilizer application and livestock production are known contributors to nutrient enrichment in agricultural surface waters (Arbuckle and Downing, 2001; Carpenter et al., 1998).

Nutrient enrichment to surface waters can be detected in several ways. The best known impact of nutrient enrichment of surface water is high algal production, or eutrophication (e.g. Dillon and Rigler, 1974; Schindler, 1977; Hecky and Kilham, 1988). In addition to aesthetic problems such as foul taste and odour, high productivity can lead to serious ecological problems such as hypoxia.

Nutrient enrichment can shift the algal community toward cyanobacterial dominance (e.g. Tilman et al., 1986; Nixdorf et al., 2003; Beisner, 1997). Cyanobacterial abundance has been correlated with increases in total phosphorus and total nitrogen (Downing et al., 2001). Cyanobacteria are often a cause for public concern due to toxins produced by some species (e.g. O'Neil et al., 2012) or blooms and hypoxia (Diaz and Rosenberg, 2008). Light limitation resulting from increased turbidity associated with eutrophication can favour cyanobacteria with buoyancy control (Scheffer et al., 1997). However, fast-growing chlorophytes have been shown to dominate some lakes where

nutrient concentrations are low but, due to continuous inputs, do not limit algal growth (Jensen et al., 1994).

Excessive nutrient enrichment can also increase variability in population abundance. Early models identified potential destabilization effects of disturbances, such as nutrient enrichment, in communities and populations (e.g. Rosenzweig, 1971). More recently, there has been empirical and theoretical evidence that disturbance can drive population-level variability (e.g. Fraterrigo and Rusak, 2008; Cottingham et al., 2000).

One way to determine whether the GA has impacted surface waters is to analyse historical records of nutrient inputs to surface waters over time, if such records exist. Keatley et al. (2011) used a paleolimnological approach to estimate diatom-inferred total phosphorus (TP) concentrations from sediment cores to determine whether there was evidence of an increase in eutrophication in lakes after the onset of the GA (~1945). Increases in TP after 1945 were more common in European than North American lakes and were largely attributed to agricultural land use. An alternate paleolimnological approach to understand eutrophication during the GA is to compare fossil pigments (proxies of plant and algal abundance) before and after 1945, to examine lake productivity rather than nutrient status. In addition to changes in total plant and algal abundance, fossil pigments provide reliable information about plant and algal community composition (Leavitt and Findlay, 1994), making it possible to examine indicators of eutrophication or disturbance such as changes in community composition, community variability (Cottingham et al., 2000) and the rate of change of community composition (Hall et al., 1999).

The goal of chapter two was to determine whether there is evidence of the GA circa 1945 in shallow lakes of southern Alberta. Evidence of the GA was expected due to sustained increases in agricultural production since the turn of the 20th century (Statistics Canada, 1966-2006) and increased consumption of fertilizer in southern Alberta at least since 1960 (Statistics Canada, no date). Both factors contribute to the high risk rating for surface water quality in much of Alberta's agricultural region (Alberta Agriculture and Rural Development, 2005).

Four outcomes were expected if the GA impacted lakes in southern Alberta. First, accelerated increases in plant and algal abundance were expected. Second, relative increases in cyanobacteria abundance were expected due to their association with eutrophication and low-light conditions. Finally, the disturbance caused by increased nutrients was expected to destabilize the primary producer community and result in increased population variability and an increased rate of change of community composition.

Alternate Clear and Turbid Regimes

Shallow lakes are ideal ecosystems for studying alternate regimes because they are relatively discrete systems and positive feedbacks in shallow lakes help to maintain alternate clear or turbid regimes. The chapter on alternate regimes (chapter three) explores whether there is evidence of alternate clear and turbid regimes among shallow, prairie lakes in southern Alberta and whether these lakes shift between regimes.

Alternate regime theory

Ecosystems were traditionally viewed as relatively static systems attracted to a single equilibrium state following perturbations. Current thinking challenges this view and suggests instead that ecosystems can be attracted to multiple states, or regimes (Holling, 1973). Theoretical models (e.g. Holling, 1973; May, 1977) provided much of the initial evidence of multiple stable regimes in ecosystems and models have been continually refined over the past four decades (e.g. Scheffer, 1990; Dent *et al.*, 2002, van Nes *et al.*, 2007; Scheffer and van Nes, 2007). Transitions between states (regime shifts) are not always gradual or linear and often there are relatively rapid and surprising shifts between ecosystem states (Carpenter, 2003). Such regime shifts occur as internal positive feedbacks associated with the initial state are suddenly overwhelmed by conditions that drive the system into an alternative regime that has its own characteristic positive feedback mechanisms that reinforce its persistence (Scheffer and Carpenter, 2003). Regime shifts are often driven by a combination of factors, including internal and/or external drivers (Carpenter, 2003).

The concept of regime shifts is often illustrated using a stability landscape model (Fig. 1.2, adapted from Scheffer and Carpenter, 2003). Possible regimes are represented by the cups, or basins of attraction, within the landscape and the position of the ball represents the possible states, or regimes, of the system within the landscape. The strength of internal feedbacks determines the shape of the landscape and the location of system thresholds to condition variables (such as nutrient concentrations shown in Fig. 1.2). Incremental changes to external drivers have the potential to move the system

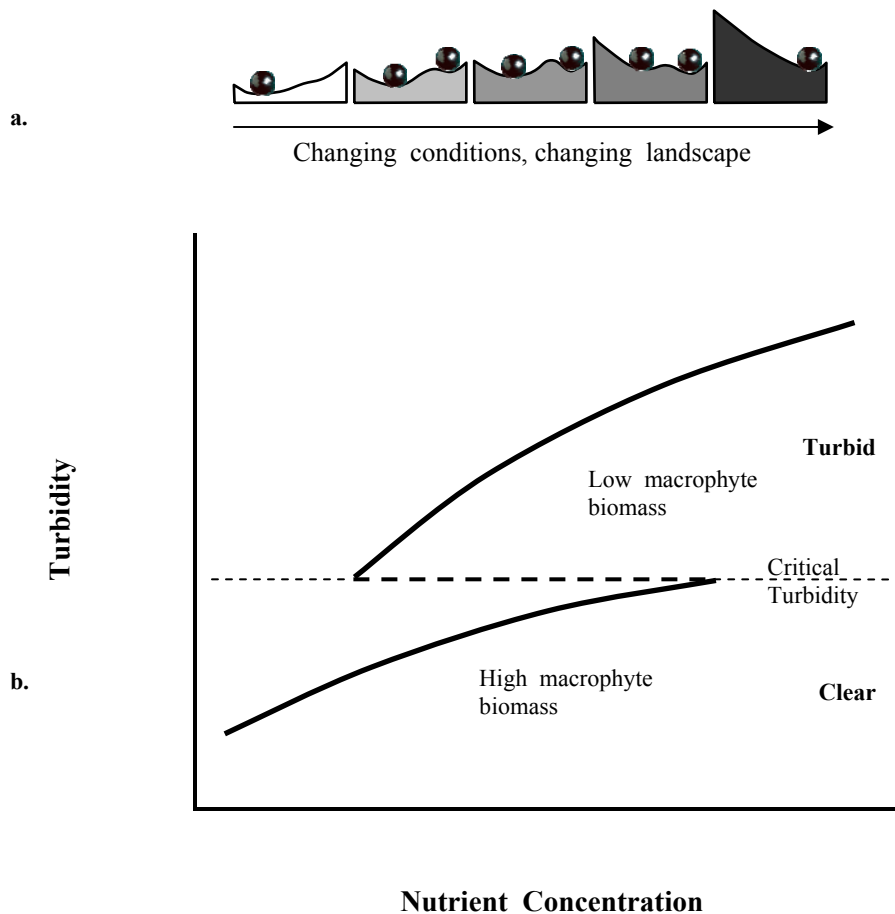


Figure 1.2. Conceptual model that illustrates alternate clear and turbid regimes in shallow lakes (adapted from Scheffer *et al.* (1993) and Scheffer and Carpenter (2003)). The ball and landscape model (a.) shows landscape progression through five phases as nutrient conditions increase. At low concentrations (far left) there is a single basin of attraction (low nutrients, clear regime) yet as nutrients increase the landscapes support alternate clear and turbid regimes. As nutrient concentrations reach very high levels (far right) the landscape only supports a turbid regime. Clear regimes are characterised by high macrophyte biomass and low phytoplankton biomass (b.). Turbid conditions are largely attributed to high phytoplankton biomass and are characterised by low macrophyte biomass. At very low and very high nutrient concentrations lakes tend to be clear or turbid, respectively. However, at intermediate nutrient concentrations clear and turbid conditions are possible.

toward system thresholds (Dent *et al.*, 2002). For example, internal feedbacks in clear lakes determine the form of the model landscape and the accumulation of phosphorus can alter the position of the ball (state or regime), moving it closer to a regime threshold beyond which the system is attracted to a turbid regime. A shift occurs when system conditions cross a threshold beyond that which the internal feedbacks can support. This could simply be a gradual progression to extreme conditions or it could be a sudden perturbation that occurs at intermediate conditions. In theoretical models, regime shifts can arise through internally generated fluctuations in the system but, in practice, regime shifts only occur when internal processes and external drivers combine to effect a change (Scheffer and Carpenter, 2003). The system is then maintained in this alternate regime by an alternate set of feedbacks.

Nonlinear behaviour associated with regime shifts results from different sets of internal feedbacks maintaining each regime. Thus, (1) similar system conditions (e.g. the same phosphorus concentrations in a lake) can exist under alternate regimes (Fig. 1.2) and (2) the threshold to regime change in one direction is not equal to the threshold for a shift in the opposite direction. This phenomenon, called hysteresis, is common in ecosystems with alternate ecological regimes (Carpenter, 2003).

Shallow lakes

Shallow lakes have been frequently used to study alternate regimes. Much of the research has focused on clear and turbid regimes (e.g. Carpenter, 2003; Jackson, 2003, Scheffer *et al.*, 1993) but additional types of shifts, such as dependant dynamics in aquatic food webs and trophic cascades (e.g. Carpenter 2003, Carpenter and Kitchell,

1993), have also been studied. Theoretical models of shallow lake systems in northern Europe (Scheffer, 1990) encouraged many to attempt to identify examples of alternate regimes in nature. Scheffer *et al.*'s (1993) lake model describes alternate clear and turbid regimes.

Clear regimes are often dominated by macrophytes, periphyton and epiphytes as primary producers (Carpenter, 2003). In cases where light penetrates deep enough, macrophytes can cover the entire bottom of a lake, help stabilize sediments from releasing phosphorus and monopolize much of the available phosphorus (Dent *et al.*, 2002). Macrophytes provide refugia to zooplankton from planktivores (Jeppesen *et al.*, 1998) and zooplankton grazing helps suppress phytoplankton biomass. Macrophytes also provide habitat to invertebrates that graze epiphytes. These positive feedbacks support the growth of further macrophyte biomass. Under turbid regimes, phytoplankton out compete macrophytes for resources (such as light and/or nutrients), zooplankton are eaten because they have nowhere to hide from predators and phytoplankton proliferate since they have been released from grazing pressure. Macrophyte loss leaves sediments more vulnerable to disturbance and mixing (Madsen *et al.*, 2001). Turbid regimes are perpetuated by algal decay which consumes oxygen, promoting anoxia which can stimulate the release of additional phosphorus from sediments. As phytoplankton biomass increases, macrophytes are less able to compete and the turbid regime positively reinforces itself. According to Scheffer *et al.*'s (1993) model, nutrient-poor shallow lakes are clear and nutrient-rich lakes are turbid. Over an intermediate range of the most limiting nutrient, however, lakes can exist in either clear or turbid regimes.

Despite internal feedbacks that reinforce alternate regimes, shifts between regimes are possible. For example, under clear conditions, phosphorus accumulates in organisms and in sediments if oxygen is abundant and macrophytes limit water column mixing. As this unavailable phosphorus accumulates internally, clear regimes become more vulnerable to internal or external perturbations that could release phosphorus and drive the system to a turbid regime (Carpenter, 2003). The size of a lake can impact the potential for internally driven regime shifts as smaller lakes have a lower capacity to sequester phosphorus and may be more susceptible to shift to and remain in a turbid state (Mayer and Rietkerk, 2004). Other drivers of regime shifts could include nutrient loading from external sources (e.g. industry, municipal wastewater, agriculture), changes in water level and seasonal changes such as ice cover and hypoxia (Scheffer and van Nes, 2007).

Scheffer and Carpenter (2003) outline three indicators of alternate regimes and regime shifts: (1) multimodal distribution of individual systems across alternate regimes, (2) dual relationship between control factors and alternate regimes, and (3) jumps in times series data that suggest a sudden shift from one regime to another. Some studies have found evidence of alternate stable regimes in shallow lakes (e.g. Scheffer *et al.*, 1993; Jackson, 2003; Zimmer *et al.*, 2009), yet others have not (Bayley and Prather, 2003; McGowan *et al.*, 2005b; Sim *et al.*, 2006a; Bayley *et al.*, 2007), suggesting that not all shallow lakes fit a clear-turbid dichotomy. Indeed, the concept of two alternate regimes in shallow lakes has been recently broadened. Additional considerations such as spatial heterogeneity within individual lakes, seasonality, non-equilibrium dynamics and differences in critical nutrient levels depending on lake characteristics all complicate how alternate regimes are manifested in shallow lakes (Scheffer and van Nes, 2007).

Empirical evidence now supports the existence of additional regimes and includes clear regimes better characterized by benthic microbial communities than benthic macrophytes (McGowan *et al.*, 2005b), lakes with floating plant dominance (O'Farrell *et al.*, 2009; Scheffer *et al.*, 2003), lakes with ample light penetration but no submerged macrophyte cover (Bayley *et al.*, 2007), and turbid lakes characterized more by suspended sediments than phytoplankton abundance (Davis *et al.*, 2010).

The purpose of chapter three was to determine whether there are indications of alternate regimes and regime shifts for shallow lakes in southern Alberta. Jackson (2003) found evidence of alternate regimes in my study area and I hypothesized that this study would provide additional support for alternate regimes in southern Alberta. Water quality data from 20 shallow lakes were used to look for a multimodal distribution among the 20 lakes to distinguish between clear and turbid states (*sensu* Scheffer and Carpenter, 2003). Water quality data were also used to determine whether nutrients control lake regimes in these lakes in the manner described by Scheffer *et al.*'s alternate regime model. Sediment core proxies from eight of the lakes were analyzed to first determine the time series of indicators of change, then whether there were jumps in the indicators consistent with abrupt changes that would signal shifts between regimes.

Salinity Effects on Turbidity

Shallow lakes in southern Alberta exhibit a striking range of salinities (Mitchell and Prepas, 1990). The lakes that I sampled ranged from 0.63 – 41.29 g/L total dissolved solids (TDS) (for reference, seawater is ~ 35 g/L TDS). In chapter four I examined how salinity is related to turbidity in shallow lakes of southern Alberta. I focussed on how salt

concentration and salt composition related to phytoplankton biomass and the proportion of heterocystous cyanobacteria in phytoplankton communities.

Salinization of agricultural lands is a growing global problem (Gordon *et al.*, 2008) that has already impacted agricultural water bodies in arid and semi-arid regions (Williams, 2001). Naturally saline lakes exist, yet agricultural practices such as irrigation and land conversion from deep rooted plants to shallow rooted pasture and crops contribute to extensive secondary salinization. Salinity increases alter biological communities, reduce biodiversity and change natural hydrologic patterns (Williams, 2002).

Much of the semi-arid prairie of southern Alberta was converted to agriculture following the late 1800s and, since 1950, there has been an increase in visible salinity on Alberta's agricultural lands (Cannon and Wentz, 2000). Anticipated increases in average annual temperature for the Calgary area range from ~2-8 °C by 2080 with only 20-50 mm of additional annual precipitation (Barrow and Yu, 2005). Increased temperatures with little additional precipitation will likely lead to greater moisture deficits and increased salinization. The prairies of Canada and the northern United States are covered with hundreds of thousands to ten million pothole lakes and wetlands (Covich *et al.*, 1997; Last and Ginn, 2005). Small lakes and wetlands are important sources of biodiversity in agricultural landscapes (Søndergaard *et al.*, 2005) and are important breeding habitat for migratory waterfowl in southern Alberta. Groundwater is an important contributor to annual water budgets in Alberta's pothole lakes, yet salinity in the lakes is also affected by high evaporation: precipitation ratios (Covich *et al.*, 1997). Southern Alberta's lakes range from fresh (TDS < 500 mg/L) to highly saline (e.g. TDS > 50 000 mg/L) due to the

combined effects of agricultural salinization of groundwater and high evaporation: precipitation ratios. Salinity impacts may become increasingly pronounced in the future as the past century has been uncharacteristically wet (Laird *et al.*, 2003).

Water's salinity characteristics shape aquatic communities. Aquatic organisms experience osmotic stress when the concentration of total dissolved solids (TDS) is high. Halo-tolerant species employ strategies such as altering intracellular concentrations of amino acids (Saros and Fritz, 2000) or other osmolytes (Hart *et al.*, 1991) that alter internal osmotic pressure. Other organisms are simply replaced by halo-tolerant species as salt concentrations extend beyond their tolerance ranges. In shallow lakes like those found in southern Alberta, organisms may also be subjected to large fluctuations in TDS over a summer resulting in community composition changes or communities dominated by organisms with wide salinity tolerance. The ion composition of salts also affects aquatic community composition. For example, high concentrations of sulphate may interfere with nitrogen fixation and the prevalence of nitrogen fixing cyanobacteria (Marino *et al.* 2003). While some diatoms are favoured in water dominated by sulphate, other diatoms are favoured in water with high bicarbonate concentrations (Saros and Fritz 2000). Sulphate and iron influence phosphorus cycling (Caraco *et al.* 1989; Clavero *et al.*, 1990; Jordan *et al.*, 2008) and metal cations such as magnesium can reduce phosphorus bioavailability through competitive binding (Waiser and Robarts 1995).

The purpose of chapter four was to determine how salt concentration and ion composition affect phytoplankton-dominated turbidity in the lakes of southern Alberta and whether these effects help explain why some shallow lakes in southern Alberta do not fit the alternate regimes model for shallow lakes (Scheffer *et al.*, 1993). Because high

salt concentrations are often associated with lower phytoplankton biomass, the hypothesis was that either total salt concentration or concentrations of particular major ions would be associated with low turbidity, even under high nutrient conditions. Several objectives were met to investigate this hypothesis. The first objective was to verify that phytoplankton biomass was low in lakes with high salt or major ion concentrations and were not related to nutrient concentrations. The second objective was to determine whether total turbidity was low in lakes with high salt concentration and was not related to nutrient concentrations. The third objective was to determine whether high sulphate concentrations were related to low abundance of heterocystous cyanobacteria, as would be expected based on Marino et al. (2003). A modified version of the alternate regimes model for shallow lakes (Scheffer *et al*, 1993) may better describe saline prairie lakes if salt concentration and ion composition do affect phytoplankton biomass.

CHAPTER TWO – ASYNCHRONOUS ONSET OF EUTROPHICATION ACROSS SHALLOW, PRAIRIE LAKES OF SOUTHERN ALBERTA

Introduction

Human population growth, coupled with increased industrial activity, has had unprecedented influence on the world's ecosystems since the industrial revolution and, especially, since the Second World War (Crutzen, 2002). The global human population has grown by more than 2.7 fold (UN, 2011) since 1950 and exponential changes associated with industrial activity since 1945, such as increases in CO₂ emissions, water use and fertilizer consumption, have led some to call this period the *Great Acceleration* (GA) (Steffen *et al.*, 2007). Industrial change has led to significant environmental challenges. In particular, human activity is reaching or has surpassed the boundaries of what the planet can withstand in terms of climate change, biodiversity loss and changes in nutrient cycling (Rockström, *et al.*, 2009).

Meeting the ever-increasing global demand for food, while minimizing environmental impacts, is a serious challenge (Foley *et al.*, 2011, Townsend and Porder, 2012). Synthetic fertilizers are applied to nutrient-depleted soils to support high intensity agriculture and the rate of fertilizer consumption has increased steadily since the mid-1900s (Steffen *et al.*, 2007). The UN Food and Agriculture Organization estimates that total fertilizer consumption, globally, more than quadrupled from 31 000 000 tonnes in 1961 to 141 000 000 tonnes in 2002 and that total meat production quadrupled between 1961 and 2010 (UN FAOStat, 2012a). Fertilizer application and livestock production are

known contributors to nutrient enrichment in agricultural surface waters (Arbuckle and Downing, 2001; Carpenter *et al.*, 1998).

Nutrient enrichment to surface waters can be detected in several ways. The best known impact of nutrient enrichment of surface water is high algal production, or eutrophication (e.g. Dillon and Rigler, 1974; Schindler, 1977; Hecky and Kilham, 1988). In addition to aesthetic problems such as foul taste and odour, high productivity can lead to serious ecological problems such as hypoxia.

Nutrient enrichment can shift the algal community toward cyanobacterial dominance (e.g. Tilman *et al.*, 1986; Nixdorf *et al.*, 2003; Beisner, 1997). Cyanobacterial abundance has been correlated with increases in total phosphorus and total nitrogen (Downing *et al.*, 2001). Cyanobacteria are often a cause for public concern due to toxins produced by some species (e.g. O'Neil *et al.*, 2012) or blooms and hypoxia (Diaz and Rosenberg, 2008). Light limitation resulting from increased turbidity associated with eutrophication can favour cyanobacteria with buoyancy control (Scheffer *et al.*, 1997). However, fast-growing chlorophytes have been shown to dominate some lakes where nutrient concentrations are low but, due to continuous inputs, do not limit algal growth (Jensen *et al.*, 1994).

Excessive nutrient enrichment can also increase variability in population abundance. Early models identified potential destabilization effects of disturbances, such as nutrient enrichment, in communities and populations (e.g. Rosenzweig, 1971). More recently, there has been empirical and theoretical evidence that disturbance can drive population-level variability (e.g. Fraterrigo and Rusak, 2008; Cottingham *et al.*, 2000).

One way to determine whether the GA has impacted surface waters is to analyse historical records of nutrient inputs to surface waters over time, if such records exist. Keatley *et al.* (2011) used a paleolimnological approach to estimate measured diatom-inferred total phosphorus (TP) concentrations from sediment cores to determine whether there was evidence of an increase in eutrophication in lakes after the onset of the GA (~1945). Increases in TP after 1945 were more common in European than North American lakes and were largely attributed to agricultural land use. An alternate paleolimnological approach to understand eutrophication during the GA is to compare fossil pigments (proxies of plant and algal abundance) before and after 1945, to examine lake productivity rather than nutrient status. In addition to changes in total plant and algal abundance, fossil pigments provide reliable information about plant and algal community composition (Leavitt and Findlay, 1994), making it possible to examine indicators of eutrophication or disturbance such as changes in community composition, community variability (Cottingham *et al.*, 2000) and the rate of change of community composition (Hall *et al.*, 1999).

The goal of this study was to determine whether there is evidence of the GA circa 1945 in shallow lakes of southern Alberta. Evidence of the GA was expected due to sustained increases in agricultural production since the turn of the 20th century (Statistics Canada, 1966-2006) and increased consumption of fertilizer in southern Alberta at least since 1960 (Statistics Canada, no date). Both factors contribute to the high risk rating for surface water quality in much of Alberta's agricultural region (Alberta Agriculture and Rural Development, 2005).

Four outcomes were expected if the GA impacted lakes in southern Alberta. First, accelerated increases in plant and algal abundance were expected. Second, relative increases in cyanobacteria abundance were expected due to their association with eutrophication and low-light conditions. Finally, the disturbance caused by increased nutrients was expected to destabilize the primary producer community and result in increased population variability and an increased rate of change of community composition.

Methods

Study area

Sediment cores were sampled from 10 shallow lakes found in the mixedgrass ecoregion of southern Alberta's prairie (Strong, 1992). All lakes are located within 50 km of Strathmore. The region is dominated by dark brown or black Chernozemic soil. The region was grazed by bison (*Bison bison bison*) historically and, since European settlement in the mid-late 19th century, has been primarily used as agricultural land. Wheat, barley and canola have been the primary crops in the area for at least the past 50 years while cattle ranching and pork production have been the primary livestock operations over the same time (Statistics Canada, 1961-2006).

Shallow lakes are defined here as permanent, lentic inland water bodies (Davis *et al.*, 2010). The 10 shallow lakes sampled are small (< 40 ha, mean = 10 ha), shallow (depth \leq 2.1 m, mean = 1.3 m) and polymictic (Fig. 2.1). The lakes sampled are geographically isolated from rivers or streams, with major inputs being rain, snowmelt and groundwater and primary loss occurring through evaporation. There are no piscivores

in the systems and brook stickleback (*Culaea inconstans*), where they occur, are the main planktivores.

Sediment cores

A sediment core was removed from the centre of the 10 lakes using a Glew Gravity Coring Device (diameter = 6 cm). All lakes were shallow, flat-bottomed, well-mixed systems so a single central core was considered representative of the entire lake (Leavitt *et al.*, 2006). To verify this, 2 additional cores were removed from 2 of the lakes (Hilton Long and Mushroom) and used to compare changes in carbon content across the three cores of each lake.

Cores were collected during the summers of 2005 (Hilton Long, Hilton West, Hilton East, Barnett and Mushroom), 2007 (Bland, Brushy and Blackbird) and 2008 (Fresnell and F3). Cores were collected from a boat then immediately sealed and wrapped in black plastic to minimize pigment degradation. Cores were sectioned under low light conditions into 0.5 cm slices after returning to the lab within 24 hours of extraction. The second, fifth and every third slice thereafter were weighed and immediately frozen in small black plastic film canisters for pigment analysis.

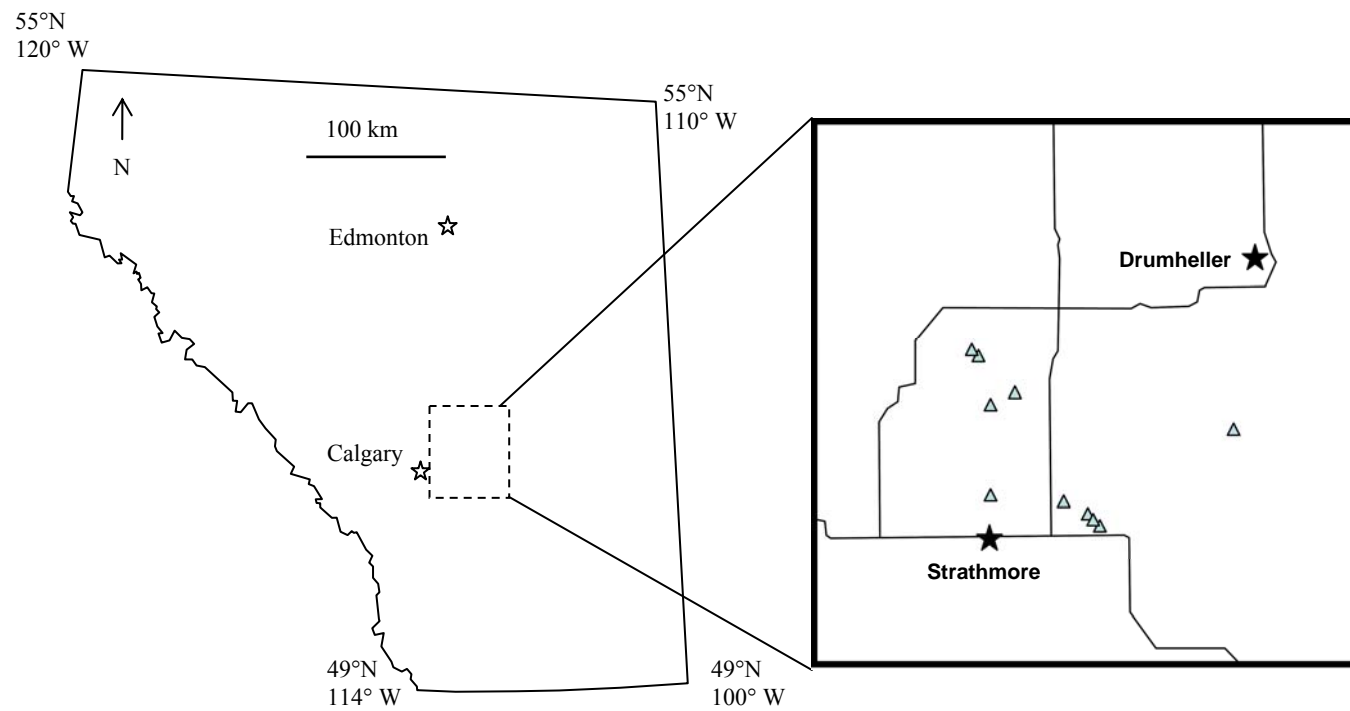


Figure 2.1. Location of 10 shallow, prairie lakes sampled (grey triangles) to examine whether there is evidence of the GA in lakes in southern Alberta.

Pigment concentrations were isolated and measured using reverse-phase high performance liquid chromatography (HPLC) following the methods outlined in Leavitt and Findlay (1994) and were used to compare plant and algal communities before and after 1945. Isolated pigments used in this study include β -carotene and pheophytin *a* (total biomass), diatoxanthin (mainly diatoms), chlorophyll *b* (green plants and algae), echinenone (cyanobacteria), canthaxanthin and myxoxanthophyll (colonial cyanobacteria), okenone (purple sulphur bacteria), fucoxanthin (siliceous algae and some dinoflagellates) and alloxanthin (crysophytes). Lutein (green plants and algae) and zeaxanthin (cyanobacteria) pigments were not completely separated during chromatography and their concentrations are therefore presented combined.

Core sediments were sent to Flett Research Ltd. (Winnipeg, Manitoba) to estimate sediment age. Sediments throughout the length of each core were freeze-dried and homogenized prior to analysis for ^{210}Pb using alpha-spectrophotometry. Because sediment accumulation rates were not constant throughout all cores, the constant rate of supply (CRS) model (Appleby and Oldfield, 1978) was used to estimate sediment age based on ^{210}Pb activity. The CRS method is considered accurate for recent sediments (60-100 years old). Due to variation in sediment deposition across lakes and over time, the number of core slices that were reliably dated from each lake varied from 4 to 19 slices, with >10 slices in most lakes. Age estimates for deeper sediments are approximations. Sediment depth was assumed to accumulate at the same rate as the sediments in the basal sediments aged using ^{210}Pb methods.

Numerical analysis

Data analyses included model fitting, segmented regressions and a one-sample *t*-test to determine the timing of productivity changes in shallow lakes of southern Alberta. Welch's approximate *t*-tests were used to compare average conditions (abundance, rate of change of relative plant and algae community composition and relative abundances of purple sulphur bacteria and cyanobacteria) across the 10 lakes before and after 1945.

Segmented regression was performed using the Segmented package (Muggeo, 2001) and Levene's median test using the Lawstat package (Noguchi, K. *et al.*, 2009) in the R language and software environment (Version 2.10; R Development Core Team, 2010). All other models and statistics were evaluated using base R.

Timing of changes

Proxies for total plant and algal abundance (β -carotene and pheophytin *a* concentrations) were used to determine whether the lakes in this study exhibited changes over the past 150 years because abundance integrates changes among all plants and algae and because increased productivity is often associated with surrounding land-use changes. Linear regression on raw and ln-transformed pigment data was used to determine whether plant and algal biomass increased since 1850 in each of the lakes.

Each lake was then examined to determine whether there was an acceleration in the increase of plant and algal abundance ca. 1945. To start, the best model describing the shapes of pigment changes over time were identified for each lake by fitting models to raw (linear regression, polynomial, exponential and segmented regression curves) and ln-transformed (linear and segmented regression) pigment data. The best model fit was

identified according to the coefficient of determination and by visual inspection of residuals. Because segmented regression provided the best fit on either raw or ln-transformed pigment data in 9 lakes, and linear regression was the best fit in the tenth, segmented regression was used to identify the timing of the most prominent changes in β -carotene and pheophytin *a* concentrations over the past ~150 years. Segmented regression estimates break-points in piecewise, linear relationships. A Davies test (Davies, 1987; Muggeo, 2001) was used to test whether slopes of individual segments within each regression were significantly different from each other to determine whether the breakpoints do represent accelerated increases in abundance. Average timing of changes in both pigments was calculated across the lakes and compared to the hypothesized break-point of 1945, the beginning of the GA, using a one-sample *t*-test.

Abundance

Mean β -carotene and pheophytin *a* concentrations were compared before and after 1945 to determine whether plant and algal abundance was significantly greater after 1945. Regression slopes for ln-transformed β -carotene and pheophytin *a* were calculated before and after 1945 for each lake. The mean of the pre-1945 slopes was compared to the mean of the post-1945 slopes using a Welch's approximate *t*-test to determine whether increases in biomass had accelerated in the post-1945 period.

Relative echinenone and okenone concentrations

Relative abundances were calculated for okenone (purple sulphur bacteria) and echinenone (cyanobacteria) concentrations within each slice of each sediment core. Relative abundance was calculated as the percentage of total pigment in the sediment. Mean relative abundance prior to and following 1945 was calculated for each lake.

Community variability

Pigment concentrations were used to compare aggregate and compositional variability (Micheli *et al.*, 1999) before and after 1945 in Hilton Long and Barnett lakes. Aggregate variability was calculated using β -carotene as a proxy for total primary producer abundance and the sum of algal carotenoids (lutein/zeaxanthin, fucoxanthin, alloxanthin, myxoxanthophyll and aphanizophyll) as a proxy for planktonic algae. Compositional variability was calculated for relative cyanobacteria abundance (relative echinenone) and relative purple sulphur bacteria abundance (relative okenone). Hilton and Barnett lakes were chosen due to relatively high temporal resolution before and after 1945 (Hilton Long = data points 2-12 years apart, Barnett = data points 4-8 years apart). Raw β -carotene and relative echinenone and okenone data were ln-transformed to remove non-intrinsic increases in variance associated with increases in pigment concentration (Lewontin, 1966). A moving average between sequential pairs of adjacent slices was used to construct local trend lines within the data, which were used as the reference from which to calculate deviation of ln-transformed pigment concentrations. Levene's median-test was used to compare variance in the data before and after 1945.

Rate change within plant and algae community

Pigments used in the rate of change calculations (lutein / zeaxanthin, diatoxanthin, chlorophyll *b*, canthaxanthin, myxoxanthophyll, echinenone, okenone, fucoxanthin, and alloxanthin) were selected based on post-depositional stability and ecological relevance. β -carotene was not selected because it is a proxy for all plants and algae rather than specific groups. Raw pigment concentrations were converted to percent of total of the selected pigment concentration for each core slice. Hellinger distance was used to calculate the magnitude of the change in relative pigment concentration between adjacent core slices (i.e. points in time) for each pigment. Hellinger distance is a metric similar to Euclidean distance but is better suited to calculating rates of change from percentage data (Lotter, 1995). Note that Lotter (1995) refers to Hellinger distance as chord distance as per Prentice (1980); in this case, chord distance is similar but not equal to Orlóci's (1967) metric of the same name. Annual rates were calculated for each time step along the sediment cores to produce a series of annual rates for each core.

Results

Timing of changes

Biomass proxies generally increased over time in 9 of the 10 lakes (Figure 2.2) – neither β -carotene nor pheophytin *a* increased significantly in Brushy Lake. Segmented regression provided the best fit on raw and ln-transformed pigment data in all lakes except Hilton West Lake, and was used to estimate the timing of the most prominent changes in β -carotene and pheophytin *a* concentrations. Timing varied across lakes and between pigments within the same lake. Hilton West and F3 lakes showed no change

points for either β -carotene or pheophytin *a* concentrations. Brushy Lake showed a breakpoint for β -carotene, but the slopes of the two segments were not significantly different ($p = 0.12$). In Bland Lake the slopes of the two segments for the regression using pheophytin *a* were not significantly different ($p = 0.13$)

Across the 7 lakes with significant breakpoints for β -carotene, the mean change point was 1932 (range: 1875 - 1975) while that for pheophytin *a* (across 6 lakes) was 1953 (range: 1912 - 1995) (Fig. 2.3). Neither break-point date was significantly different from 1945 (β -carotene: $t = 0.94$, $df = 7$, $p = 0.39$; pheophytin *a*: $t = 0.62$, $df = 6$, $p = 0.56$). However, there was a large range among the break-points for both β -carotene and pheophytin *a*.

Abundance

On average, mean β -carotene ($t = 5.7$, $df = 15$, $p < 0.0001$) and pheophytin *a* ($t = 2.1$, $df = 9$, $p = 0.032$) concentrations across the 10 lakes were greater after 1945 than before. Both pigments increased in concentration since 1850 for 9 of the 10 lakes (Fig. 2.2; β -carotene concentrations only). The onset of pigment increase varies across lakes – while some have experienced gradual increases since the late 1800s (e.g. Hilton West, Barnett) the onset in other lakes has been more recent (e.g. Hilton East, Fresnell). This variability of onset is reflected in the segmented regression analyses used to identify timing of change. In Brushy Lake, concentrations have been variable over time with no discernable trend since 1850.

Mean slopes of regression lines were significantly greater after 1945 for β -carotene ($t = 2.7$, $df = 9.3$, $p = 0.025$) and pheophytin *a* ($t = 2.4$, $df = 8$, $p = 0.041$).

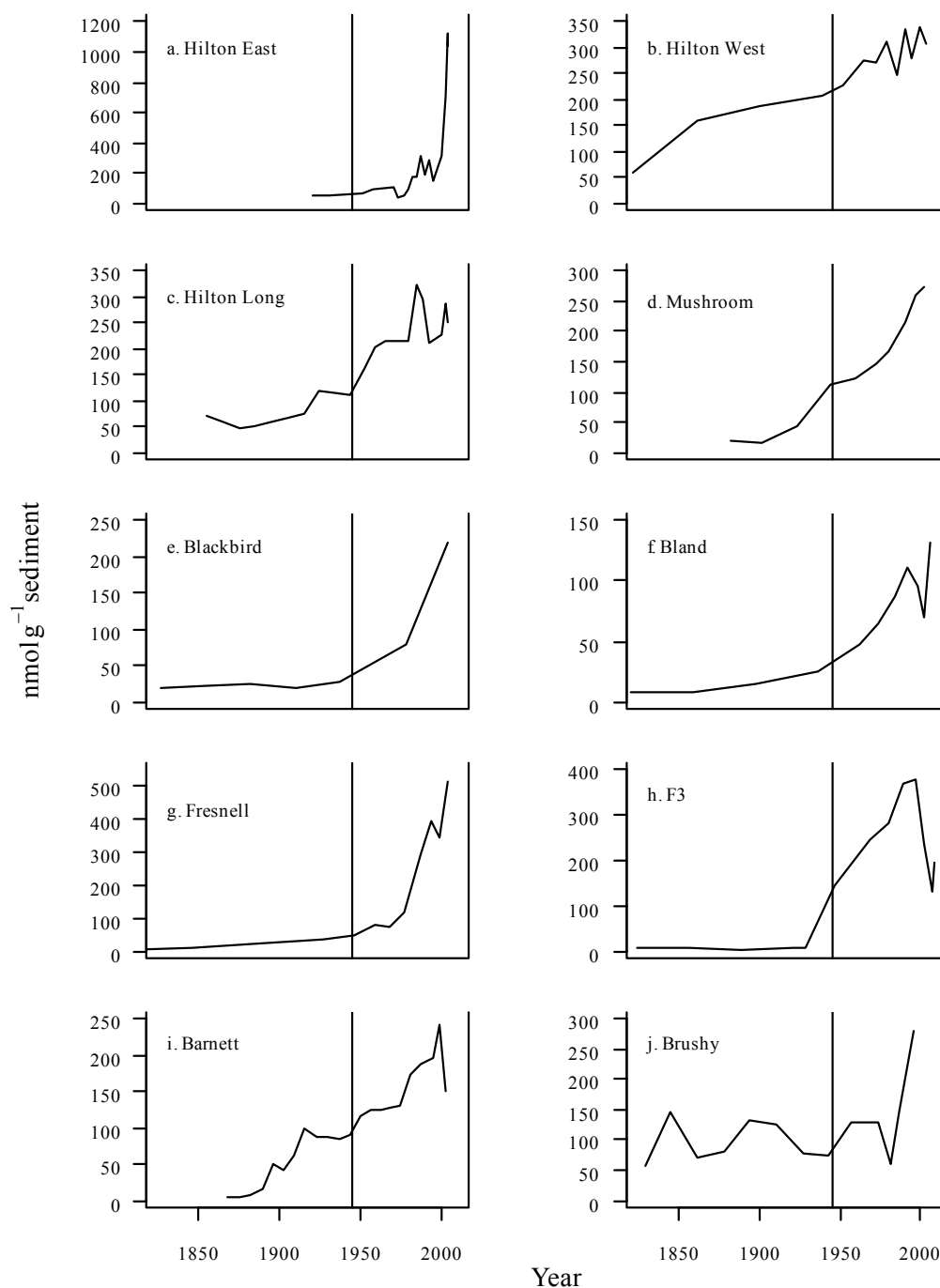


Figure 2.2. Trends in plant and algal abundance (β -carotene concentrations) in the study lakes between 1850 – 2008 based on fossil pigment analyses. Horizontal lines mark the onset of the GA (1945) (Steffen, 2007).

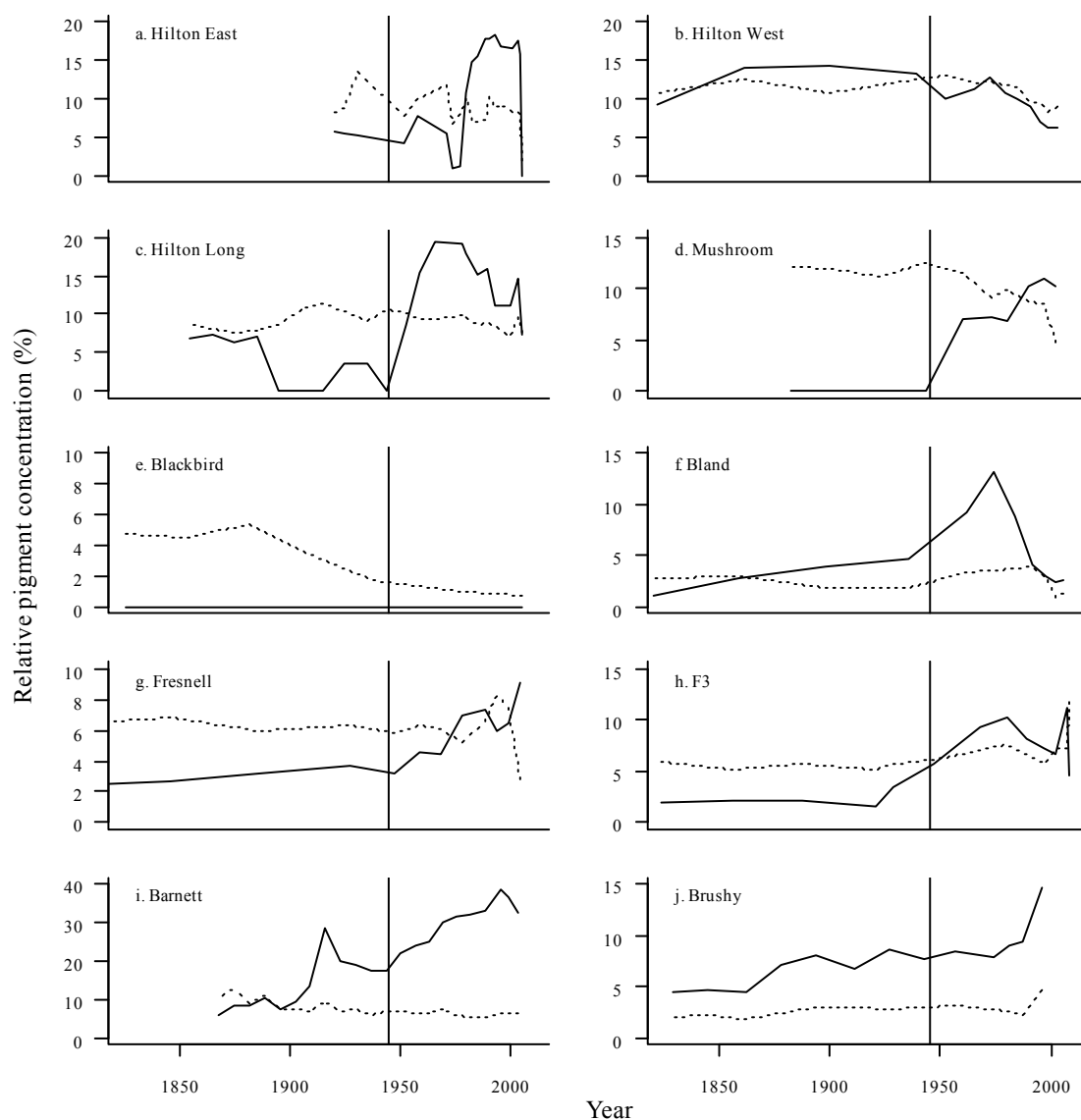


Figure 2.4. Trends in relative abundances of total cyanobacteria (echinenone; dotted lines) and purple sulphur bacteria (okenone; solid lines) in the study lakes between 1850 – 2008 based on fossil pigment analyses. Horizontal lines mark the onset of the GA (1945).

Community variability

β -carotene concentrations were not significantly more variable in Hilton Long nor Barnett lakes following 1945. Variability in the sum of algal carotenoids was significantly greater after 1945 in Hilton Long Lake ($W = 3.8$, $p = 0.028$) but there was no difference before and after 1945 in Barnett Lake. Variability of relative echinenone ($W = 14.3$, $p < 0.0001$) and okenone ($W = 4.5$, $p = 0.032$) concentrations were significantly different before and after 1945 in Barnett Lake but, contrary to expectations, variability was greater before 1945. Variability of relative echinenone concentrations were not significantly different before and after 1945 in Hilton Long Lake, but relative okenone concentrations were significantly more variable ($W = 6.4$, $p = 0.0085$) before 1945 (Fig. 2.5).

Rate of change within the plant and algal community

Mean rate of change in plant and algal community composition across the 10 lakes was significantly greater after 1945 ($t = 2.2$, $df = 10$, $p = 0.028$). Rate of change is shown graphically as the average annual rate of change over the range of years represented by each core segment. Rate of change did not increase and does not change in synchrony with β -carotene concentrations in all lakes (e.g. Barnett, Blackbird) (Fig. 2.6).

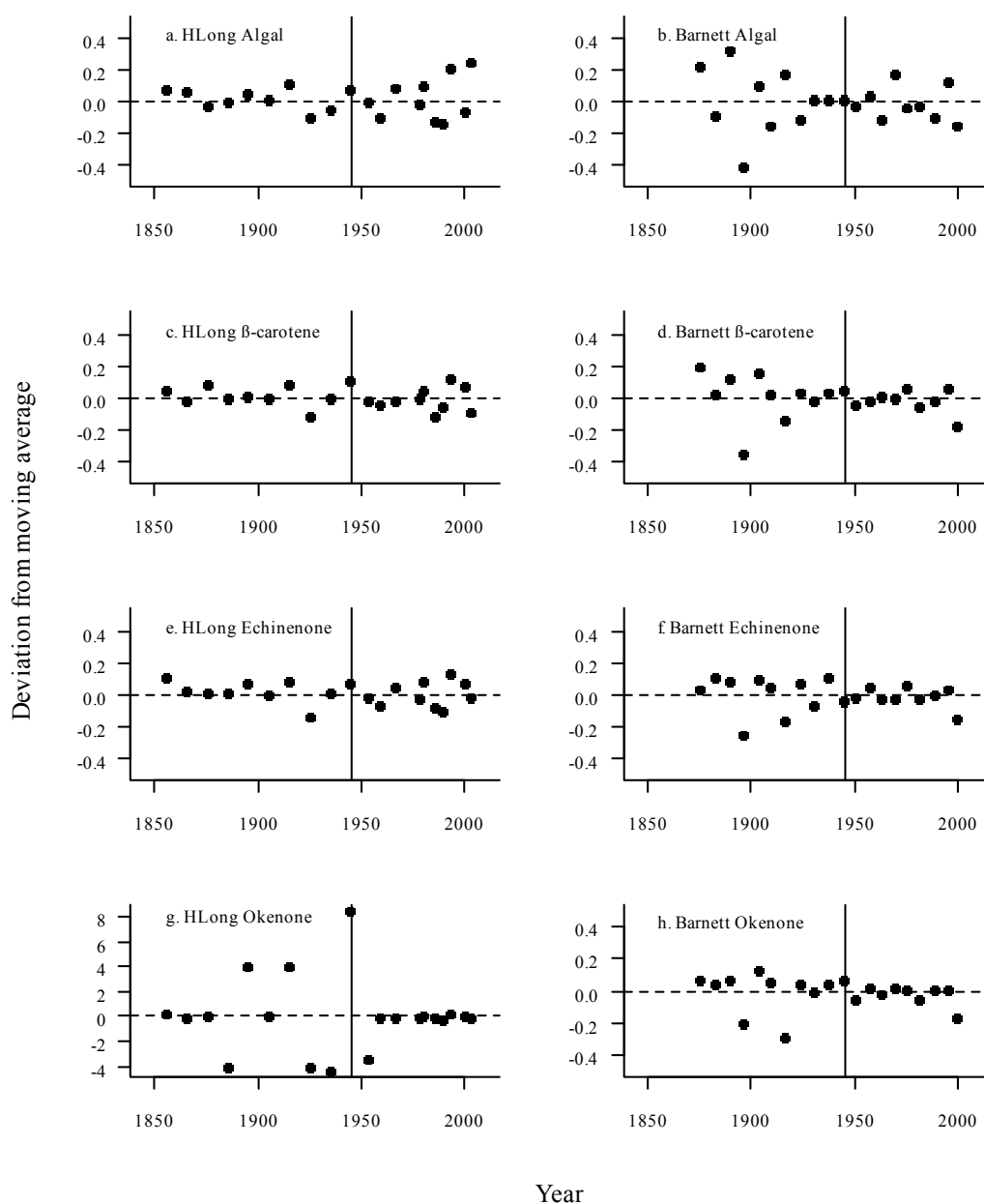


Figure 2.5. Variability in algal abundance (sum of algal carotenoids; panels a,b) plant and algal abundance (β -carotene; panels c and d), relative cyanobacteria abundance (panels e, f) and relative purple sulphur bacteria abundance (panels g,h) in the study lakes between 1850 – 2008. Variability is the deviation of pigment concentration, or relative concentrations (echinenone, okenone), from a local central tendency. Horizontal lines mark the onset of the GA (1945). Note the change in scale in panel e.

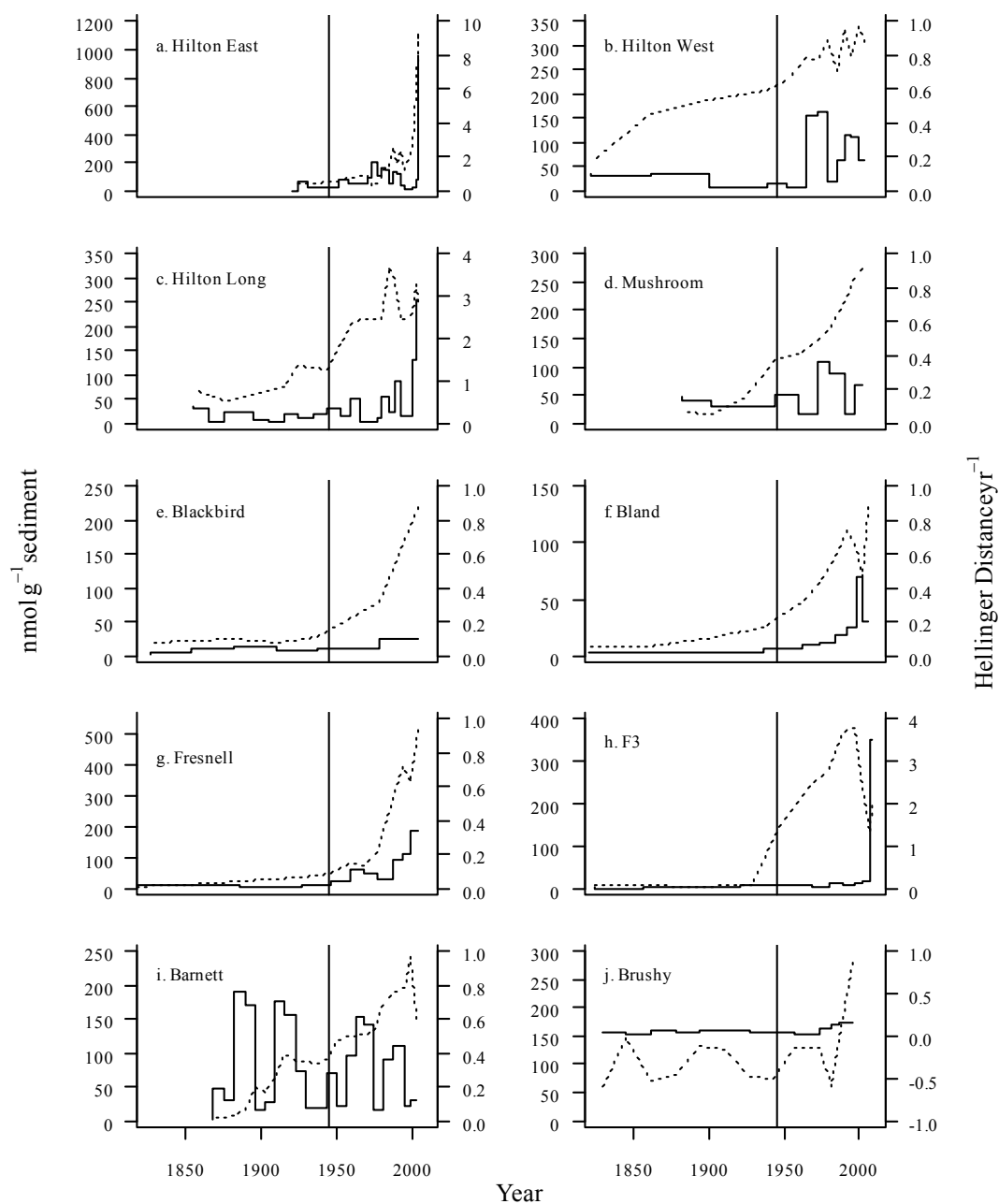


Figure 2.6. Trends in plant and algal biomass (β -carotene concentrations; dotted lines) and rates of change in plant and algal community composition (solid lines) in the study lakes between 1850 – 2008 based on fossil pigment analyses. Horizontal lines mark the onset of the GA (1945).

Discussion

There is little evidence of the GA ca. 1945 in shallow lakes of Southern Alberta. Though the mean timing of accelerated increases in phototroph abundance was not significantly different from 1945, onset of acceleration in individual lakes ranged over 50 years prior to 50 years following the GA (Figs 2.2, 2.3). Paleolimnological evidence does indicate that most lakes have become more eutrophic since 1850, but there isn't sufficient evidence to identify a punctuated, regional disturbance, as may be expected with the GA. The mean relative abundance of total cyanobacteria did not increase significantly in the lakes after 1945, though cyanobacteria dominance is often associated with eutrophic conditions. The mean relative abundance of purple sulphur bacteria was greater after 1945 and this may be due to increased production and decomposition at the sediment-water interface. No measures of community variability increased in Barnett Lake, but there was an increase in variability of planktonic algal pigments in Hilton Long Lake and this may indicate a shift between benthic and pelagic primary productivity (Cottingham et al., 2001). There was no increase in the rate of change within the primary producer community after 1945. Together, these results provide little support for a disturbance circa 1945 associated with the GA in the shallow lakes of southern Alberta. These results indicate that increases in primary production were widespread in the study area over the past 150 years but that the onset of eutrophication varied across lakes.

Timing of changes

The proposed onset of the GA, ca. 1945, corresponds with the average timing of accelerated increase in abundance in seven of the lakes studied. However, three of the study lakes did not show significant acceleration in abundance and across the remaining seven lakes the onset of acceleration ranged from 1875 to 1995. In three lakes the acceleration occurred before 1930 and, therefore, the onset of acceleration cannot be attributed to a GA circa 1945. Onset of accelerated increases in abundance circa 1945 or anytime following 1945 could be interpreted as signs of increased industrial activity that began with the GA in the study area. However, only three lakes show accelerated increase in plant and algal abundance circa 1945 at the lake level. These results are not surprising as Keatley *et al.* (2011) found a small proportion of the North American lakes in their study demonstrated accelerated eutrophication circa 1945.

Abundance

Plant and algal abundance was greater and the increases in abundance were faster after 1945, yet the onset of accelerated increase in abundance differed across lakes. Similar overall trends with large differences in timing suggest that external, regional factors have had a long-term influence on biomass within the lakes but that either (1) these external influences were introduced to different areas of the study region at different times or that (2) internal lake dynamics moderated the impacts of external influences differently across the lakes.

There is evidence that external factors such as land-use and climate impact water quality in the northern Great Plains of Saskatchewan (Hall *et al.*, 1999). Temperature and

precipitation have not changed appreciably in the study region since the late 19th century (Environment Canada, no date; Appendix A, Fig. A.1), but there have been continuous increases in the area of seeded cropland and total number of cattle in Alberta over the past 100 years, coinciding with increases in plant and algal abundance. It is plausible that nutrients from agricultural run-off could be affecting abundance in each of these prairie lakes – all of which are currently surrounded by farmland. Agriculture is a known contributor to surface water eutrophication (Arbuckle and Downing, 2001; Carpenter *et al.*, 1998) and surface water quality in the study region is classified as being at high risk according to Alberta Agriculture and Rural Development (2005).

Brushy Lake was the only lake that did not show a significant increase in biomass since 1850. Water column sampling in 2007/ 2008 showed that Brushy Lake was extremely hypereutrophic (chlorophyll *a* = 276 µg / L) and the phytoplankton community was dominated by colonial, heterocystous cyanobacteria. This lake may have been hypereutrophic since 1850, which could explain why human impacts have had little influence on plant and algal biomass in Brushy Lake. Most of the increase in Brushy Lake's total plant and algal concentrations occurred ca. 1990 and, while concentrations have nearly doubled since 1990, it is most likely that Brushy was hypereutrophic even then since half of the 2007/2008 chlorophyll *a* concentrations = 138 µg / L.

Relative echinenone and okenone concentrations

Higher relative echinenone concentrations had been expected in the study lakes after 1945 because cyanobacteria, especially nitrogen-fixing cyanobacteria, are frequently more prominent in nutrient enriched lakes (Nixdorf *et al.*, 2003; Downing *et al.*, 2001)

and increased echinenone (as a proxy for cyanobacteria) has also been associated with eutrophication (Leavitt and Findlay, 1994). The study lake catchments contain cropland and pasture, both of which would contribute nutrients to the lakes (Arbuckle and Downing, 2001). Water quality sampling in 2007 indicated that all lakes would be considered eutrophic or hypereutrophic based upon TN and most would be considered the same in terms of TP (Chapter 4). It is possible that only a fraction of total nutrients are biologically available in these lakes (Chapter 4) and this may explain why expected changes were not observed in relative cyanobacteria abundance. It is also possible that fast-growing chlorophytes dominated over slower-growing cyanobacteria in these shallow lakes if their high nutrient supplies were continuous (Jensen *et al.*, 1994). Due to differences in cellular carotenoid quotas across species (Leavitt and Findlay, 1994) and within species under varying light conditions (MacIntyre *et al.*, 2002) changes in species composition or environmental conditions could also affect the relative abundance of echinenone in cyanobacterial cells. Alternatively, it is possible that another nitrogen-fixing organism that is well-adapted to low-light conditions, such as purple sulphur bacteria (Lindstrom *et al.*, 1950; Casamayor *et al.*, 2008), was able to compete with cyanobacteria for limiting resources.

Okenone is a carotenoid pigment specific to chromatiaceae bacteria that is used in paleolimnology as a proxy for purple sulphur bacteria and is often used as an indicator of anoxic conditions (Overmann, 1993). Purple sulphur bacteria depend on sulfides as electron donors during photosynthesis, reducing CO₂ and oxidizing sulfides to sulphate in the process (Jørgensen and Postgate, 1982), and sulfides do not exist under oxic conditions. As a result, purple sulphur bacteria are restricted to a narrow habitat range in

lakes where there are sufficient quantities of light and sulfides. In deep, stratified lakes this is the pelagic oxic-anoxic interface but in shallow, polymictic lakes these conditions occur within the upper sediments (Jørgensen and Postgate, 1982). The sediment-water interface of shallow, productive lakes will be anoxic due to heterotrophic decomposition as long as sediments are not suspended into the water column and provide suitable conditions for purple sulphur bacteria as long as sufficient light reaches them.

Relative okenone concentrations were examined because, after initial data exploration, it was clear that relative okenone concentrations had changed more than other relative pigment concentrations. It is unlikely that higher okenone concentrations indicated winter anoxia since light limitation and low temperatures would likely prevent purple sulphur bacteria blooms (Jörg Overmann, pers.comm.). Low relative okenone conditions were not associated with high turbidity either; okenone concentrations and the ultraviolet radiation index were inversely related, showing that purple sulphur bacteria were able to thrive even when light conditions at the sediments were at their lowest. Others have also found that purple sulphur bacteria do not require high light conditions (Casamayor *et al.*, 2008; Jørgensen and Des Marais, 1986). On the other hand, raw okenone and β -carotene concentrations shared strikingly similar trajectories over time (excepting Blackbird Lake) (Appendix A, Fig. A.2). Relative okenone rarely represents greater than 20% of group-specific pigments, suggesting that the relationship is not likely driven by okenone. Increased plant and algal abundance (β -carotene), however, would lead to greater decomposition at the sediment-water interface that would enhance anoxia. Under anoxic conditions the hydrogen sulphide released from decomposition becomes a

potential source of sulphide to support purple sulphur bacteria biomass (Jørgensen and Postgate, 1982).

Community variability

Community variability did not indicate a disturbance circa 1945 for Barnett Lake but provided weak evidence for a disturbance in Hilton Long Lake. If there was a disturbance in these lakes ca. 1945, one would expect lower variability before 1945 and greater variability after. Neither of the two proxies used as indicators of aggregate community variability (total primary producer abundance as β -carotene and algal abundance as the sum of algal pigments) increased in Barnett Lake after 1945. When aggregate community variability does not increase following disturbance, compositional or population variability may still increase (Fraterrigo and Rusak, 2008). However, there was no evidence of increased compositional variability (echinenone for total cyanobacteria and okenone for purple sulphur bacteria) in Barnett Lake either. While there is no evidence of disturbance to the lake circa 1945 based on pigment variability, there has been an increase in primary producer abundance (β -carotene) since the late 1800s (Fig. 2.2). It is possible that this increase was due to a gradual increase in primary producer abundance, including macrophytes, suggesting that the GA has not affected water clarity in this lake.

The results for Hilton long Lake may indicate a shift between benthic and pelagic sources of primary production. Total primary producer abundance (β -carotene) did not show increased variability but there was significantly greater variability in the sum of algal pigments after 1945. Similar results following a fertilization experiment were

interpreted by Cottingham *et al.* (2001) as a possible shift between benthic and pelagic production. Compositional variability was not significantly greater for either total cyanobacteria (echinenone) or purple sulphur bacteria (okenone). Again, Cottingham *et al.* (2001), found similar results where, following a fertilization experiment, there was no increase in total cyanobacteria variability despite increases in abundance. Like Barnett Lake, Hilton Long Lake has shown signs of eutrophication since the late 1800s including increases in primary producer abundance (Fig. 2.2). However, Hilton Long Lake was highly eutrophic in 2007 (Table 1, Chapter 4). It is possible that a punctuated disturbance associated with the GA, such as increased fertilizer application, may have contributed to accelerated eutrophication in the lake ca. 1945 and may have contributed to increased variability in planktonic algal abundance.

An alternate interpretation of the data is that when variability was greater before 1945 it may have been an early-warning signal that the system was reaching a critical threshold (Carpenter and Brock, 2006), such as a threshold between clear and turbid lake regimes. However, other dynamics can cause a decrease in variability of system variables, such as a decrease in algal biomass during transition to cyanobacterial dominance (Carpenter *et al.*, 2009), making it difficult to interpret the signals unless the underlying system dynamics are well understood. It seems unlikely that high variability before 1945 in the data is an example of an early warning signal of a critical threshold since the resolution between data points is relatively coarse (5 – 10 years) for Hilton Long and Barnett lakes prior to 1945. This coarse level of resolution could mask more finely resolved variability that could be associated with eutrophication due to time averaging (Cohen, 2003). Early warning signals, such as increased variability, have

primarily been studied using theoretical models and there may be barriers to their application in ecological forecasting (Hastings and Wysham, 2010).

Rate of change within plant and algal community

Greater average rate of change in community composition since 1945 is consistent with the expectation that human impacts would have a destabilizing effect on the lake communities. Potential destabilizing effects of disturbances, such as nutrient enrichment, (e.g. Rosezweig, 1971; Steiner, 2005) on communities and populations continue to be well-studied. One possible effect of community instability is increased rate of change in community composition. Instability in the rate of change is related to increases in variability (described above) in that both address the magnitude of changes in pigment concentrations, but rate of change also incorporates a temporal component to identify how quickly change is occurring. Increased rates of change in plant and algal community composition have also been observed following agricultural disturbance in aquatic ecosystems in Saskatchewan (Hall *et al.*, 1999).

Rate of change calculations represent the sum of relative changes in stable and ecologically relevant pigments over time. Therefore, high rates of change do not necessarily indicate a continual progression toward a particular (e.g. cyanobacteria dominated) community, but could equally indicate oscillations between two or more community types. Also, the pigment approach taken here does not address changes in specific species but species groups (e.g. diatoms, cyanobacteria, green plants). Visual inspection of the individual pigment data for each lake was used to determine which relative pigment concentrations showed trends over time. Increases in relative abundance

of purple sulphur bacteria (okenone) was the most prominent trend in most lakes while other lakes showed no obvious trends in relative pigment concentration over time.

Similar to the biomass results, increases in the rate of change were asynchronous across the study lakes, again suggesting that external stressors to water quality were either moderated by internal forces that differed across lakes or that external stressors were introduced locally at different points in time (Fig. 2.3). Surprisingly, changes in biomass and changes in rates of community composition change are not synchronous. Proxies used to represent abundance (β -carotene) and rate of change (a multivariate calculation using numerous pigments) are both community level measures and while complete synchrony might not be expected, results from Barnett and Blackbird lakes are clearly unrelated. Water column sampling in both of these lakes showed that they had relatively low phytoplankton abundance (chlorophyll *a*: Barnett = 1.06 $\mu\text{g/L}$; Blackbird = 6.49 $\mu\text{g/L}$) in 2007, near their peak abundance since 1850. Large fluctuations in the rate of community composition change in Barnett Lake is not likely due to shifts between clear and turbid conditions because plant and algal biomass has consistently increased since 1850 and recently peaked during a time when the lake was known to be clear (Jackson, 2003). Periods of rapid change are associated with large fluctuations in colonial cyanobacteria (myxoxanthophyll) which have dampened over time, indicating that Barnett Lake has experienced periods of relatively abundant cyanobacteria but that these “blooms” were never very large since overall plant and algal biomass has always been low.

Rates of community composition change have remained very low throughout the history of Blackbird Lake and these data would support a hypothesis that it has remained

in a relatively clear regime over time. The relatively large increases in abundance in Blackbird Lake may better reflect extremely low biomass in early years rather than high abundance currently. The increasing abundance since 1945 coincides with increasing relative abundance of chlorophyll *b* (unpublished data) and relative abundance of other pigments have primarily remained constant. This may reflect increasing macrophyte biomass rather than changes to the green algal biomass, which would be consistent with observed mesotrophic conditions in 2007.

Conclusion

There is no conclusive evidence of the GA ca. 1945 in shallow lakes of southern Alberta. Mean timing of accelerated increases in plant and algal abundance was not significantly different from 1945, but the onset of acceleration in individual lakes spanned 100 years. Most lakes have become more eutrophic since 1850, but there isn't sufficient evidence to identify a punctuated, regional disturbance, as would be expected with a GA. The relative abundance of total cyanobacteria did not increase significantly in the lakes after 1945, but the relative abundance of purple sulphur bacteria did. No measures of community variability increased in Barnett Lake, but there was an increase in variability of planktonic algal pigments in Hilton Long Lake and this may indicate a shift between benthic and pelagic primary productivity. There was no increase in the rate of change of community composition within the primary producer community after 1945. These results provide little support for a disturbance circa 1945 associated with the GA in the shallow lakes of southern Alberta. Instead, these results indicate that increases in primary

production were widespread in the study area over the past 150 years but that the onset of eutrophication varied across lakes.

CHAPTER THREE: LIMITED EVIDENCE OF ALTERNATE REGIMES IN ALBERTA'S SHALLOW, SOUTHERN PRAIRIE LAKES

Introduction

Over the past 35 years there has been considerable interest in the possibility of alternate regimes in natural ecosystems (e.g. May, 1977) and that some ecosystems may undergo sudden, sometimes unexpected, shifts from one regime to another (Scheffer *et al.*, 1993; Jackson, 2011). The theory behind alternate regimes is well developed (Scheffer, 1990; Scheffer and Carpenter, 2003; Scheffer and van Nes, 2007; Scheffer *et al.*, 2009), yet, in practice it has been notoriously difficult to demonstrate definite examples of alternate regimes in nature (Scheffer and Carpenter, 2003), largely because one must demonstrate that mechanisms that maintain alternate regimes or are associated with regime change are not simply the maintenance or rapid change of key environmental variables. Scheffer and Carpenter (2003) outline three indicators of alternate regimes and regime shifts: (1) multimodal distribution of individual systems across alternate regimes, (2) dual relationship between control factors and alternate regimes, and (3) jumps in times series data that suggest a sudden shift from one regime to another.

Shallow lakes have been frequently used to study alternate regimes. Theoretical models of shallow lake systems (Scheffer, 1990) encouraged many to attempt to identify examples of alternate regimes in the field. Scheffer *et al.*'s (1993) lake model describes alternate clear and turbid regimes (Fig. 3.1). The clear regime is dominated by macrophytes that promote clear water by mechanisms that stabilize sediments and provide refugia for the large zooplankton that most effectively graze phytoplankton.

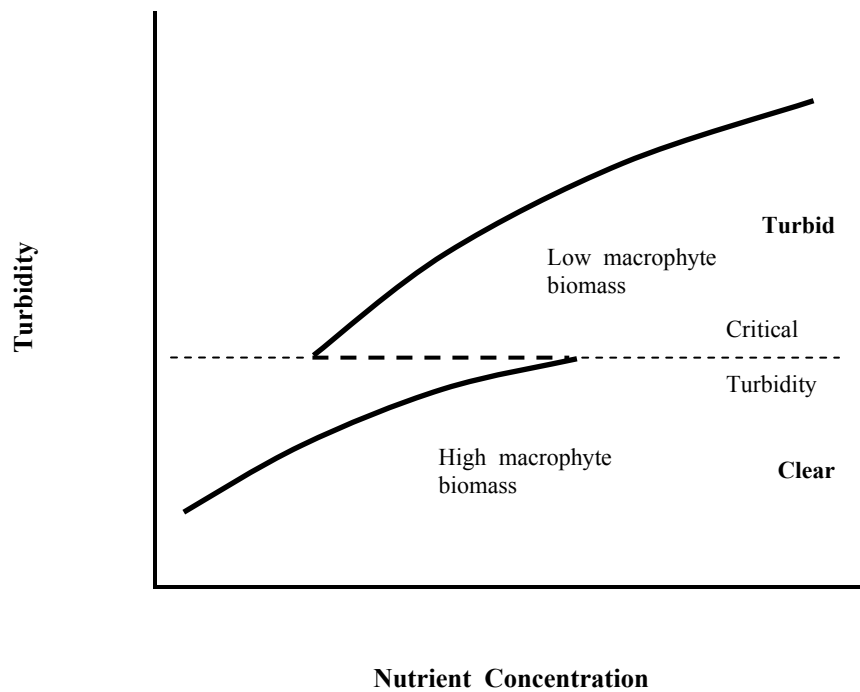


Figure 3.1. Conceptual model of conditions that describe alternate clear and turbid regimes in shallow lakes. Adapted from Scheffer *et al.* (1993). Clear regimes are characterised by high macrophyte biomass and low phytoplankton biomass. Turbid conditions are largely attributed to high phytoplankton biomass and are characterised by low macrophyte biomass. At very low and very high nutrient concentrations lakes tend to be clear and turbid, respectively. However, at intermediate nutrient concentrations both clear and turbid conditions are possible.

Lakes in turbid regimes are phytoplankton-dominated and maintain high turbidity due to sediment resuspension and by outcompeting macrophytes for light and nutrients (Scheffer, 1990; Scheffer *et al.*, 1993). According to the Scheffer *et al.*'s model, nutrient-poor shallow lakes are clear and nutrient-rich lakes are turbid. Over an intermediate range of the most limiting nutrient, however, lakes can exist in either clear or turbid regimes. Some studies have found evidence of alternate regimes as described by Scheffer *et al.* (1993) in shallow lakes (e.g. Scheffer *et al.*, 1993; Jackson, 2003; Zimmer *et al.*, 2009), yet others have not (Bayley and Prather, 2003; McGowan *et al.*, 2005b; Sim *et al.*, 2006a; Bayley *et al.*, 2007), suggesting that not all shallow lakes fit a clear-turbid paradigm.

The conceptual model of two alternate regimes in shallow lakes has been recently broadened. Additional considerations such as spatial heterogeneity within individual lakes, seasonality, non-equilibrium dynamics and differences in critical nutrient levels depending on lake characteristics all complicate how alternate regimes are manifested in shallow lakes (Scheffer and van Nes, 2007). There is growing empirical evidence that supports the existence of additional regimes. Evidence includes clear regimes better characterized by benthic microbial communities than benthic macrophytes (McGowan *et al.*, 2005b), lakes with floating plant dominance (O'Farrell *et al.*, 2009; Scheffer *et al.*, 2003), lakes with ample light penetration but no submerged macrophyte cover (Bayley *et al.*, 2007; Bayley and Prather, 2003), and turbid lakes characterized more by suspended sediments than phytoplankton abundance (Davis *et al.*, 2010).

The purpose of this study was to determine whether there are indications of alternate regimes and regime shifts for shallow lakes in southern Alberta. Jackson (2003) found evidence of alternate regimes in my study area and I hypothesized that this study

would provide additional support for alternate regimes in southern Alberta. Water quality data from 20 shallow lakes were used to look for a multimodal distribution among the 20 lakes to distinguish between clear and turbid states (*sensu* Scheffer and Carpenter, 2003). Water quality data were also used to determine whether nutrients control lake regimes in these lakes in the manner described by Scheffer *et al.*'s alternate regime model. Sediment core proxies from eight of the lakes were analyzed to first determine the time series of indicators of change, then whether there were jumps in the indicators consistent with abrupt changes that would signal shifts between regimes.

Methods

Study area

During August, 2007, I sampled 20 shallow lakes from the mixedgrass ecoregion of southern Alberta's prairie (Strong, 1992). All lakes were located within a 125 km radius of Strathmore (Fig. 3.2). The land is dominated by dark brown or black Chernozemic soil. The region was grazed by bison (*Bison bison bison*) historically and, since European settlement in the mid-late 19th century, has been primarily used as agricultural land. Plants that use the C4 photosynthetic pathway, such as Blue grama grass (*Bouteloua gracilis*), tend to be the most prevalent native vegetation under the frequently dry conditions (Adams *et al.*, 2004; Adams, pers. comm., 2010). Wheat, barley and canola have been the primary crops for at least the past 50 years (Statistics Canada, 1961-2006); these plants use the C3 photosynthetic pathway. Cattle ranching, followed by pork production, have been the primary livestock operations over the same time period (Statistics Canada, 1961-2006).

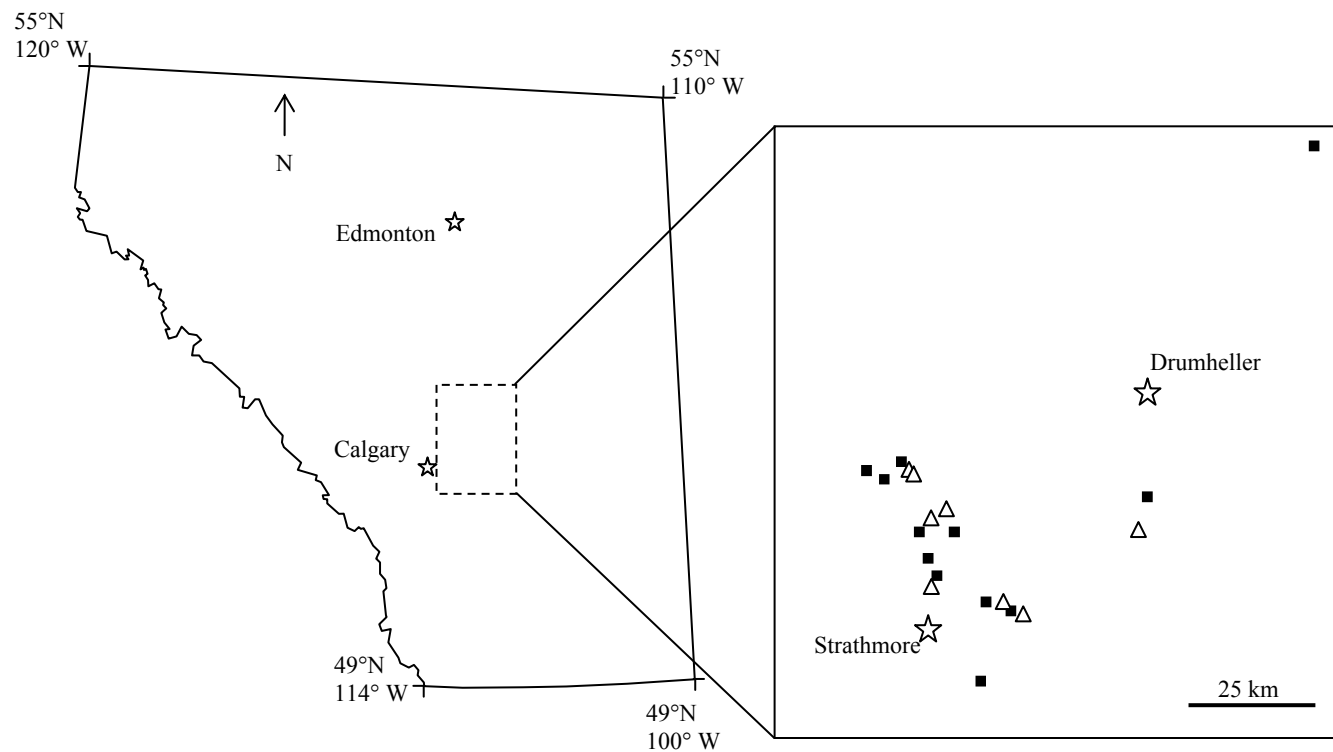


Figure 3.2 Study area within the mixed grass ecoregion of southern Alberta. Water samples were taken from 20 shallow lakes (black squares and open triangles). Sediment cores were taken from 8 of these lakes (open triangles).

Shallow lakes are here defined as permanent, lentic inland water bodies, as per Davis *et al.* (2010). The 20 lakes are small (< 40 ha, mean = 7 ha), very shallow (depth ≤ 2.7 m, mean = 1.0 m) and polymictic. They range in salt concentration from fresh (< 500 mg/L) to highly saline (41.3 g/L). Salt composition is variable, but tends to be dominated by sodium, sulphate and/or bicarbonate. The lakes sampled are geographically isolated from rivers or streams, with major inputs being rain, snowmelt and groundwater and primary loss occurring through evaporation. There are no piscivores in the systems and brook sticklebacks (*Cluaea inconstans*), where they occur, are the main planktivore.

Field and laboratory methods

Water samples

Water samples were collected from the 20 lakes during the last 2 weeks of August, 2007 to assess water chemistry and phytoplankton community composition. All samples were collected from the centre of each lake directly from the water column at 0.5 m depth, except where $Z_{\max} < 0.5$ m in which case samples were taken from mid-depth. Samples for phytoplankton enumeration and alkalinity were collected in 240 ml glass bottles. Phytoplankton samples were filled leaving ~ 10 ml air space and treated immediately with several drops of Lugol's solution. Two additional phytoplankton samples were collected at randomly selected sites at either end of each lake. Alkalinity samples were collected by submerging bottles and filling them to the top then closing them underwater with air-tight caps to ensure no air bubbles were present within the samples. The remaining water samples were collected with 1 L Nalgene® bottles at a depth of 0.5 m (mid-depth if $Z_{\max} < 0.5$ m) directly from the water column. Bottles used to

collect samples for ion analyses were washed and rinsed at least seven times with de-ionized water. Bottles for the remaining water samples were washed, acid-bathed and then rinsed with distilled water. All samples were kept on ice in dark coolers until they reached the lab.

Temperature, conductivity, dissolved oxygen and pH were measured directly in the field in the centre of each lake at 0.5 m depth (mid-depth if $Z_{\max} < 0.5\text{m}$) using a Hydrolab mini-sonde equipped with a Surveyor 4 data logger. Secchi depth was measured for each lake, but the disc was often visible at maximum depth because lakes are so shallow. Turbidity was measured using an Orbeco-Hellige (model 966) portable turbidity meter.

Nutrient and chlorophyll *a* samples were analysed or preserved within 24 hours of sampling to avoid degradation. Total nitrogen (TN) and total carbon (TC) samples were refrigerated (4°C) immediately and then analyzed with ion chromatography (Dionex ICS-1000 Ion Chromatography System) within 28 days of collection. Total phosphorus (TP) and soluble reactive phosphorus (SRP) were analysed within 24 hours using the molybdate blue method (Strickland and Parsons, 1968).

Chlorophyll *a* water samples (between 25-350 ml per sample) were filtered through Whatman GF/C filters under minimal light. Chlorophyll *a* was extracted from filters into acetone using standard methods (Strickland and Parsons, 1968) and quantified fluorometrically with correction for phaeopigments.

Total suspended solids (TSS) were measured to assess the components of lake turbidity. Between 250-1250 ml of water were filtered through pre-weighed and labelled GF/F filters (0.7µm pore size). Samples were dried overnight in a drying oven (60 °C)

and then weighed to determine weight of suspended solids. Organic matter was determined by loss on ignition at 550°C.

Major anions and cations were measured to assess total dissolved solids (TDS) and relative ion composition for each lake. Following collection, ion samples were immediately preserved, if needed, and refrigerated (4°C) after returning to the lab. Cation samples were filtered through a 0.45 µm syringe filter, acidified with enough HNO₃ to bring the sample pH below 2 prior to refrigeration. Sodium, potassium and calcium concentrations were analysed using ion chromatography (Dionex ICS-1000 Ion Chromatography System) while magnesium concentrations were measured using an atomic absorption spectrometer (Perkin-Elmer Analyst 100). Alkalinity, sulphate, and chloride samples did not require preservation and were analyzed by ion chromatography. Nitrate and nitrite samples were acidified with H₂SO₄ to pH < 2 prior to refrigeration and then measured using continuous flow analysis (CFA) in a Technicon AutoAnalyzer. Carbonate and bicarbonate were calculated from titration endpoints that were measured using an Orion Autochemistry 960 Autotitrator. All ion samples were analyzed within 28 days of collection.

Sediment cores

A sediment core was removed from the centre of eight of the 20 lakes using a Glew Gravity Coring Device (diameter = 6 cm). All lakes were shallow (≤ 2.7 m), flat-bottomed, well-mixed systems so a single central core was considered representative of the entire lake. To verify this, 2 additional cores were removed from 2 of the lakes

(Hilton Long and Mushroom) and used to compare changes in carbon content across the three cores of each lake.

Cores were collected during the summers of 2005 (Hilton Long, Hilton West and Mushroom), 2007 (Bland, Brushy and Blackbird) and 2008 (Fresnell and F3). Cores were collected from a boat then immediately sealed and wrapped in black plastic to minimize pigment degradation. Cores were sectioned under low light conditions into 0.5 cm slices after returning to the lab within 24 hours of extraction. The second, fifth and every third slice thereafter were weighed and immediately frozen in small black plastic film canisters for pigment analysis. All other slices were sealed in plastic bags and refrigerated (4°C) in dark plastic bins prior to analysing oospore abundance.

Pigment concentrations were measured using reverse-phase high performance liquid chromatography (HPLC) following the methods outlined in Leavitt and Findlay (1994) to identify changes in total algal and phytoplankton abundance over the length of the sediment cores. Total plant and algal abundance was approximated using β -carotene concentrations and lutein/zeaxanthin concentrations were used as a proxy for cyanobacteria/green algae. β -carotene is a carotenoid pigment found in both plants and algae that is frequently used as an indicator of plant and algal abundance (e.g. Carpenter and Leavitt, 1991; Leavitt and Findlay, 1994; Hall *et al.*, 1999; McGowan *et al.*, 2005b). Lutein and zeaxanthin are pigments indicative of green plants and algae and cyanobacteria, respectively (Leavitt and Hodgson, 2001). The two pigments co-elute during chromatographic analysis and are reported together. They were used here as an indicator of changes in phytoplankton abundance because green algae and cyanobacteria often dominate phytoplankton communities under eutrophic conditions (Jensen *et al.*,

1994, Watson *et al.*, 1997). Changes in lutein/zeaxanthin and other individual algal carotenoid concentrations were compared to changes in the sum of total algal carotenoids (Cottingham *et al.*, 2000) over time.

Elemental composition and stable carbon and nitrogen isotopes were analysed to determine sediment sources and sediment age throughout the length of the cores. ^{210}Pb dating was performed by Flett Research Ltd. (Winnipeg, Manitoba). The constant rate of supply (CRS) model (Appleby and Oldfield, 1978) was used because sediment accumulation rates were not constant throughout all cores; this method is considered accurate for recent sediments (60-100 years old). Dates for older sediments are approximations; they were extrapolated based on the least recent time span between modelled sediments. Total carbon, total nitrogen and total carbon isotope ratios in core sediments were measured using an elemental analyzer (Carlo Erba NA 1500) coupled to an isotope ratio mass spectrometer (Finnigan MAT delta plus XL) in continuous flow mode.

Macrophyte oopsoids were collected from the sectioned, wet sediments to estimate changes in macrophyte abundance over the length of the cores. Sediment disaggregation methods were based on recommendations from Alwynne Beaudoin (Royal Alberta Museum, Edmonton, Alberta) and Dr. Alison Smith (Kent State University, Kent, Ohio). Sediment volume for each sample was measured using displacement of deionized water in a 200 ml graduated cylinder. Sediment mass for each sample was measured as the mass added to the water and cylinder. Each sediment sample was poured, with accompanying water, into a labeled 1 L Nalgene® bottle. Approximately 500 ml of hot ($\sim 90^\circ\text{C}$) deionized water was poured over the sediments

and 5 ml of baking soda were immediately added. The solution was mixed gently and left to stand. When the solution was cool, 5 ml of Calgon® (sodium tripolyphosphate, carbonic acid and sodium salt) were added and the solution was stirred again, covered with foil, then left to sit overnight. The following day, sediments were gently rinsed through a stack of three 8-inch sieves (500 μm , 125 μm and 63 μm mesh openings). If sediments were still aggregated, they were completely frozen, thawed and then rinsed through the sieve stack a second time. Each of the three sieve fractions were rinsed into separate petri dishes and refrigerated. All fossils were removed within 5 days of refrigeration, then frozen for storage.

Numerical analysis

All statistical analyses were performed using the R language and software environment (Version 2.10) (R Development Core Team, 2010). The Rioja package (Juggins, 2009) was used in the R software environment to perform cluster and broken stick model analyses. All other calculations were performed using the base R environment.

Bimodal Distribution

Lakes were clustered using Ward's minimum variance method, a hierarchical, agglomerative clustering method (Legendre and Legendre, 1998), to determine whether there were discrete clear and turbid clusters among the 20 lakes sampled. A linkage between two clusters increases the variance within the new cluster, but Ward's method attempts to minimize the increase in variance within clusters as linkages are made. Here,

the increase in total variability associated with cluster linkages was compared to the increase in variability that would be expected by a broken-stick model (Bennett, 1996). Cluster linkages were noteworthy if the increase in total variability within the data was greater than expected from the broken-stick model. Noteworthy cluster linkages identify potential thresholds between clear and turbid regimes.

Before clustering, lakes were sorted in numerical order by turbidity or chlorophyll *a*, and extreme values were removed. Though extreme values are not normally removed from data before statistical analysis, they were removed here because cluster analysis was used to identify bimodal distributions indicative of alternate clear and turbid regimes. When data from all 20 lakes were included, clusters separated lakes with extremely high values from those with lower values, though it was obvious that many of the lakes within the “low” value cluster were not clear. Eliminating extreme data from the lakes allowed cluster analyses to partition the lakes into groups that were more likely to represent clear and turbid regimes. Extreme data were identified using Dixon’s Q test. For turbidity, values greater than 90 NTU were removed (4 lakes) and for chlorophyll *a*, values greater than 200 µg/L were removed (1 lake).

Dual Relationship

Correlations assessed relationships between nephelometric turbidity and chlorophyll *a* concentration, and nutrient concentrations to determine whether lakes responded to nutrients as expected under an alternate regimes model. Correlations were used instead of linear regressions because nutrients were not the sole drivers of water clarity in these lakes (Moquin and Jackson, unpublished data). According to theory

(Scheffer *et al.*, 1993), shallow lakes could exist in either clear or turbid regimes under intermediate nutrient concentrations and one could expect evidence of dual nutrient-turbidity relationships for a sample of lakes at intermediate nutrient concentrations. Most of the lakes sampled in this region had high nutrient concentrations that would normally be associated with eutrophic or hypereutrophic conditions (e.g. Wetzel, 2001), making it impossible to test for dual nutrient-turbidity relationships under intermediate phosphorus and nitrogen concentrations. Instead, Spearman's Rank correlations were used to test whether turbidity increased with nutrients, as would be expected under the model, for lakes within high nutrient concentration ranges, which were operationally defined as TP >100 µg/L (16 lakes) and TN >2000 µg/L (17 lakes) to reduce the chances of including lakes that could be considered to have intermediate nutrient concentrations. All correlations were ranked because rank correlations test for similar order between variables rather than linear relationships between variables and turbidity is expected to increase with nutrients, but not necessarily linearly.

Linear regression between chlorophyll *a* concentration and turbidity was used to determine whether phytoplankton abundance drives turbidity in the 20 study lakes. Natural log transformations were performed on the data prior to analysis to better meet the assumptions of linear regression (Sokal and Rohlf, 1981).

Jumps in Time Series

Chronologically constrained cluster analysis (Grimm, 1987) coupled with the broken-stick model (Bennett, 1996) was used to identify substantial breaks in the fossil pattern of eight sediment cores, which represent time periods when lakes may have

shifted between regimes. Five proxies were selected to identify clear versus turbid periods within the cores (Table 3.1). Lutein/zeaxanthin and β -carotene were used as indicators of green algae/cyanobacteria and total plant and algal abundance, respectively. *Chara spp.* oospores were used as indicators of macrophyte abundance because charophytes are the dominant modern macrophyte in the study lakes and their oospores preserve well relative to remains from other modern macrophytes found in the lakes such as *Potamogeton spp.* (Davidson *et al.*, 2005). Atomic C/N ratios were used to identify changes in macrophyte and phytoplankton abundance because macrophytes have a greater carbon to nitrogen ratio than phytoplankton (Cross *et al.*, 2000). $\delta^{13}\text{C}$ was used to identify changes between phytoplankton and macrophyte productivity due to lower $\delta^{13}\text{C}$ values for phytoplankton compared to macrophytes. A limited number of indicators were used to minimize ambiguity in the results. When possible, there is balanced representation between algal and macrophyte proxies to minimize bias in the clusters.

Data analyses were restricted to sediments from 1850 and younger. First, proxy data were transformed to range between 0 - 1 because the indicators were measured in different units and on different measurement scales. Data were then clustered based on a Euclidean dissimilarity matrix using Rioja (Juggins, 2009).

Broken-stick analysis (Bennett, 1996) was again to identify noteworthy cluster linkages that accounted for greater variability than expected. Noteworthy cluster linkages were used to identify potential jumps between clear and turbid regimes. Because the broken stick model will always identify some breaks as greater than expected and some as less than expected, unless observed increments in sums of squares exactly match

Table 3.1. Expected changes in sediment core proxies used to identify transitions between clear and turbid periods for eight shallow, prairie lakes in southern Alberta.

Proxy	Phytoplankton-dominated Turbid	Macrophyte-dominated Clear	Comments
Oospores	↓	↑	Oospores are durable charophyte propagules.
$\delta^{13}\text{C}$	↓	↑	$\delta^{13}\text{C}$ is more negative in phytoplankton (~ -25 to -30) compared to macrophytes (e.g. > -10).
C/N	↓	↑	Free-floating phytoplankton have relatively low carbon: nitrogen ratios (~ 4 to 10) compared to macrophytes (>15) and land plants (C_3 plants >15; C_4 plants >35).
Lutein / Zeaxanthin	↑	↓	Proxy for green algae/ cyanobacteria abundance.
B-carotene	↑	↑	Proxy for total plant and algal abundance.

Sources: Davidson *et al.*, 2005; Cohen, 2003; Cross *et al.*, 2000; Leavitt and Findlay, 1994

expected values, noteworthy cluster linkages may simply indicate the biggest changes within each core and may not indicate true shifts between clear and turbid regimes.

Qualitative assessment of each core was used to further determine whether rapid changes (jumps) between alternate regimes likely occurred.

Results

Bimodal distribution between clear and turbid lakes

Lakes clustered according to turbidity fell into 3 clusters when lakes with extremely high values were removed (Fig. 3.3). The most distinct cluster linkage separated the 5 most turbid lakes, ranging from 53.6 – 66.0 NTU. The remaining lakes were separated into two clusters; 5 lakes with lowest turbidity values (1.1 – 5.6 NTU) and 7 lakes with intermediate values (11.8 – 40.6 NTU).

Lakes clustered according to chlorophyll *a* concentrations fell into 3 clusters when the most extreme chlorophyll *a* value was removed, although the lakes in these clusters differed from those in the turbidity clusters described above. The most distinct clusters separated the 4 lakes with the highest concentrations of chlorophyll *a* (44.1 – 97.8 µg/L) from the remaining lakes (chlorophyll *a* concentrations of 0.857 - 27.1 µg/L). The remaining lakes were then clustered by a linkage that introduced only slightly more variability than predicted (Fig. 3.3, panel d). Four lakes fell into the intermediate cluster based on chlorophyll *a* concentrations (16.2 – 27.1 µg/L) and 11 lakes formed the cluster with the lowest chlorophyll *a* concentrations (0.857 – 11.0 µg/L).

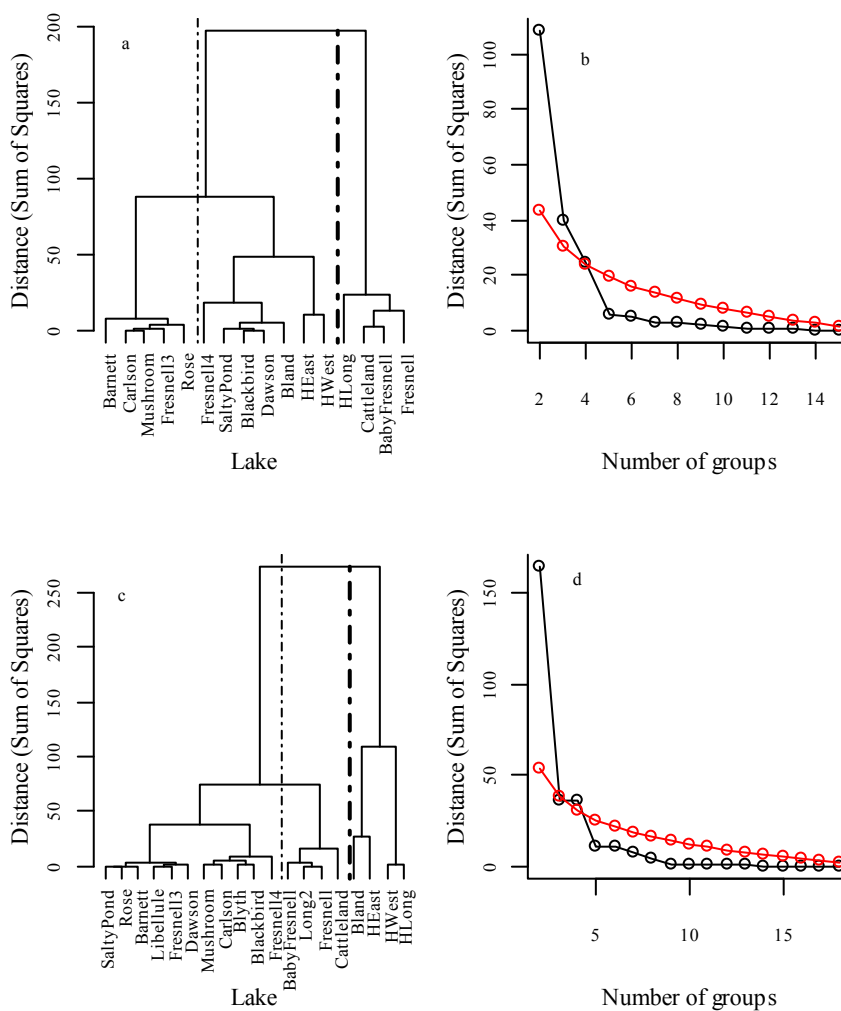


Figure 3.3. Cluster dendrograms and corresponding graphs comparing the reduction in the variability (sum of squares) of the data when clusters were linked to the reduction that would be expected from the broken-stick model. Lakes were clustered by turbidity (panels a, b) and by chlorophyll *a* (panels c, d). Dashed lines on the dendrograms indicate the cluster breaks, as identified by the broken stick model. Thick dashed lines on each dendrogram (panels a and c) indicate the most prominent breaks in the data. Lakes were arranged in order from lowest to highest turbidity or chlorophyll *a*, respectively.

Dual relationship

Do nutrients drive turbidity in these lakes?

There was no evidence that nutrients drive turbidity in these lakes. Spearman's rank correlations were used to describe the relationship between nutrients, lake turbidity and chlorophyll *a* concentrations. Spearman's rank correlations between TP and turbidity ($p = 0.00012$, $\rho = 0.77$), chlorophyll *a* ($p = 0.34$, $\rho = 0.22$), and the percentage of organic matter found in total suspended solids ($p = 0.037$, $\rho = -0.47$) confirmed that total phosphorus was more closely associated with turbidity than the organic components of turbidity. Surprisingly, when Brushy Lake was removed from the analysis due to its extreme chlorophyll *a*, TP was negatively correlated with chlorophyll *a*. TN was not significantly correlated with turbidity, chlorophyll *a* or the percentage of organic matter found in total suspended solids.

Among the high nutrient lakes, only TP was significantly, though only moderately, positively correlated with turbidity ($p = 0.025$, $\rho = 0.56$). Neither TN nor TP were significantly correlated with chlorophyll *a*.

Are turbid regimes dominated by phytoplankton?

Turbidity was not dominated by phytoplankton across all 20 lakes sampled in southern Alberta. When turbidity was regressed on chlorophyll *a* there was a significant but weak ($p = 0.018$, $R^2 = 0.27$, $n=20$) (Fig. 3.4) relationship. Suspended sediments in over half of the lakes were dominated by inorganic matter rather than organic plankton and inorganic matter tended to dominate TSS in the more saline lakes (Fig. 3.5).

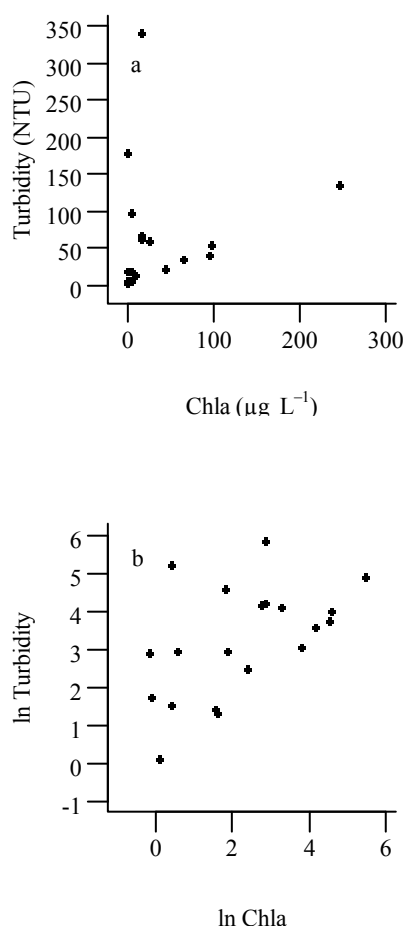


Figure 3.4. Relationship between chlorophyll *a* and turbidity in 20 shallow lakes in southern Alberta. Panel A. Untransformed data. Panel B. ln-transformed data.

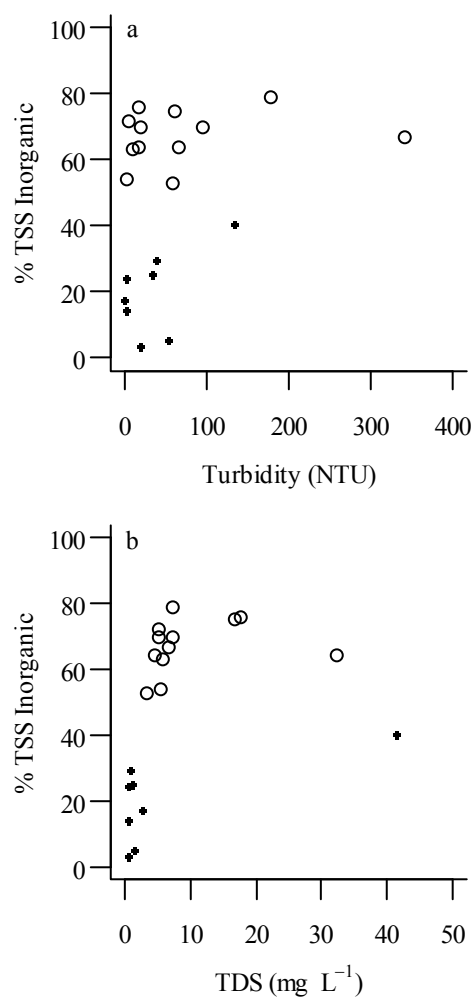


Figure 3.5. Relationship between the proportion of inorganic TSS and turbidity (panel a) and TDS (panel b) in 20 shallow lakes in southern Alberta. Open circles indicate lakes where > 50% TSS is inorganic, closed circles indicate lakes where < 50% TSS is inorganic.

Jumps in time series

Most lakes showed similar changes in isotope and pigment proxies throughout the length of the sediment cores (Figure 3.6, Appendix B). Clustering, coupled with broken stick analysis, identified the most noteworthy breaks in the fossil record for each lake of the eight lakes. In general, lutein/zeaxanthin and β -carotene concentrations were higher in recent sediments and gradually became lower in older sediments. Brushy Lake was an exception. Lutein/zeaxanthin and β -carotene concentrations were variable throughout the length of the Brushy Lake core and lutein/zeaxanthin concentrations, in particular, were high. Both C/N ratios and $\delta^{13}\text{C}$ generally declined in increasingly recent sediments for all lakes except Hilton Long where both proxies varied little throughout the length of the core. C/N ratios in the most recent sediments for all lakes were between 10-20. Oospores were only detected in 5 lakes and trends were variable across lakes.

In Mushroom Lake, the cluster breaks were associated with increases in phytoplankton pigments in the sediments. The cluster break along the F3 sediment core was associated with the appearance of phytoplankton pigments and a sharp decline in the C/N ratio as well as $\delta^{13}\text{C}$. Unlike the other lakes, F3 had no record of background levels of phytoplankton pigments prior to the 1940's. Phytoplankton pigments increased directly following the cluster break in Fresnell Lake while the C/N ratio and $\delta^{13}\text{C}$ continued a gradual decline. The Bland Lake core showed an abrupt decline in oospores following the cluster break and a relatively rapid increase in phytoplankton pigments. There was a spike in oospore abundance and $\delta^{13}\text{C}$ following the cluster break in the Hilton Long core. The C/N ratio continued a gradual decline while phytoplankton pigments continued to increase. The most prominent break in the Blackbird Lake

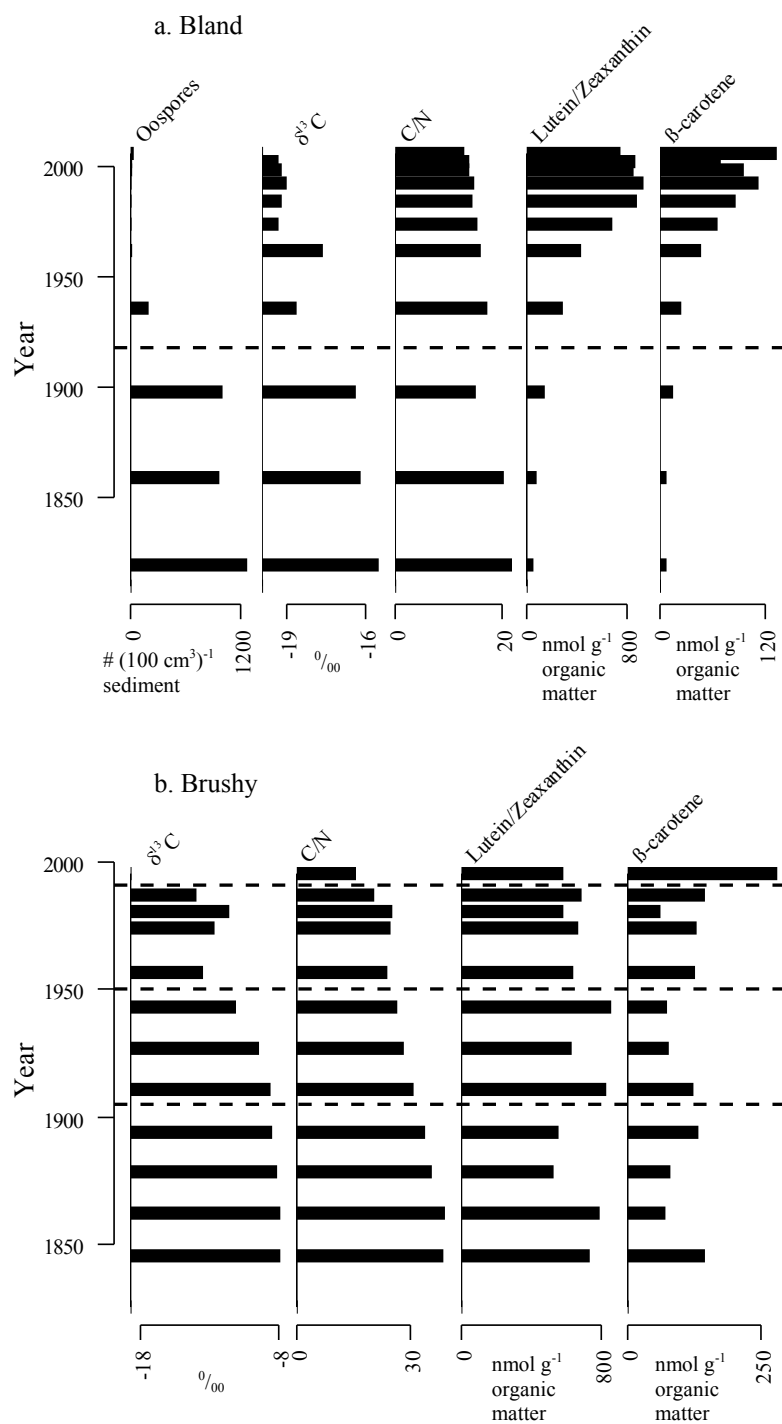


Figure 3.6. Historical changes in sediment proxies from 1850 to present in Bland Lake (panel A) and Brushy Lake (panel B). Proxies presented include oospores (abundance in 100 cm³ sediment), $\delta^{13}\text{C}$ (‰), C/N ratio, Lutein/Zeaxanthin (nmol g⁻¹ organic matter) and β -carotene (nmol g⁻¹ organic matter). Stratigraphs for all eight lakes are available in Appendix B.

sediment record was followed by a sharp decline in oospore abundance and a stark increase in the concentrations of phytoplankton pigments. Both the C/N ratio and $\delta^{13}\text{C}$ continued a gradual decline.

Two lakes showed multiple cluster breaks. Hilton West showed 2 potential breaks. The most recent break was associated with a continued decline in $\delta^{13}\text{C}$ and slight increases in phytoplankton pigment concentration. The least recent break, ca. 1850, was associated with the appearance of phytoplankton pigments, a decline in the C/N ratio and oospores and an increase in $\delta^{13}\text{C}$. There were 3 potential breaks in the Brushy core and each break accounted for little more variation than the broken-stick model, suggesting that these breaks are not likely associated with large changes in water column turbidity and were more likely related to the overall variability in the lake than in lakes where cluster breaks accounted for a greater deviation from the broken-stick model.

Discussion

There was no evidence of alternate clear and turbid regimes in the shallow lakes sampled in southern Alberta using contemporary water quality data using the three criteria of Scheffer and Carpenter (2003), but paleolimnological analysis of eight lakes indicated the possibility of regime shifts in some lakes. Contemporary water quality from 20 shallow lakes showed no signs of bimodality in the frequency distribution of clear and turbid states. The absence of a bimodal distribution results, at least in part, because phytoplankton did not dominate turbidity in most lakes. Rather than nutrients driving phytoplankton-dominated turbidity, it is likely that suspended sediments enhanced internal nutrient loading in many lakes. As a result, there was no evidence of a dual relationship between nutrients and turbidity either. Sediment cores from five of the lakes

showed transitions between lake characteristics associated with clear water regimes and those associated with turbid water regimes. These results suggest the possibility that regime shifts between clear and turbid regimes may have occurred in these lakes over the past 150 years. Due to low resolution and extensive time-averaging within cores it is not possible to determine whether increasing turbidity was associated with gradual changes or “sudden” regime shifts (*sensu* Scheffer and Carpenter, 2003) in these lakes.

Bimodal distribution between clear and turbid lakes

There was no obvious bimodal distribution between alternate clear and turbid regimes for the lakes sampled. Under a bimodal distribution, one would expect the lakes to cluster into high and low turbidity groups with few or no lakes in between. Here, the lakes clustered by turbidity fell into three statistically distinct groups; 5 clear lakes, 5 turbid lakes and 7 lakes (greater than 1/3 of the lakes in the analysis) in an intermediate turbidity cluster (Fig. 3.3). One could argue that only two clusters legitimately exist since the cluster partition between the second and third clusters accounts for only slightly more variability than expected under the broken-stick model. However, the turbidity values for the “clear” lake cluster would range 1.1 - 40.6 NTU, whereas Jackson (2003) found that turbid lakes in the same region had turbidity values ≥ 3.7 NTU and Davis *et al.* (2003) identified 10 NTU as the threshold between turbid and clear lakes in Western Australia.

Lakes were not bimodally distributed when chlorophyll *a* was clustered and this was because turbidity in most lakes was not dominated by phytoplankton. Again, there were 3 distinct lake groups; 4 lakes with high chlorophyll *a* concentrations (>44 $\mu\text{g/L}$) that are distinct from the other lakes and then an intermediate (4 lakes; 16.2 – 27.1 $\mu\text{g/L}$)

and a low (11 lakes; $<11.0 \mu\text{g/L}$) chlorophyll *a* group that are only slightly distinct from each other, based on the broken-stick model results. These results correspond reasonably well with the thresholds that Zimmer *et al.*, (2009) identified using k-means cluster analyses with Minnesota lakes. They identified $22 \mu\text{g/L}$ chlorophyll *a* as the upper threshold for most clear lakes and $31 \mu\text{g/L}$ as the lower threshold for most turbid lakes. However, the $18 \mu\text{g/L}$ threshold that Bayley *et al.* (2007) identified for lakes in northern Alberta falls within the intermediate lake cluster identified here. From an ecological perspective, one might expect clear lakes to be oligotrophic ($<2.6 \mu\text{g/L}$) or possibly mesotrophic, and turbid lakes to correspond to eutrophic ($7.3 - 56 \mu\text{g/L}$) and hypereutrophic conditions in terms of chlorophyll *a* concentration. Here, both the high and intermediate clusters correspond with eutrophic and hypereutrophic lakes based on Carlson's Trophic Index (Carlson and Simpson, 1996) while the "low" chlorophyll *a* group spans oligotrophic to eutrophic conditions. Unless eutrophic lakes can rightly be considered "clear", the statistical clustering approach taken here does not identify a bimodal distribution of clear and turbid lakes along a chlorophyll *a* continuum.

There was no bimodal distribution for either turbidity or chlorophyll *a* because turbidity was not dominated by chlorophyll *a* in most lakes and, therefore, nutrients did not drive turbidity, as would be expected under the Scheffer *et al.* (1993) model for shallow lakes. Instead, turbidity was dominated by suspended inorganic sediments in most lakes and this was most common among the more saline lakes. The extent of sediment suspension is regulated, in part, by macrophytes, but many other factors such as bioturbation, depth, fetch and wind strength also contribute (Scheffer, 1998).

Dual relationship

Due to very high nutrient concentrations in lakes across the study region of southern Alberta, it was not possible to identify a dual relationship between nutrients and turbidity at intermediate nutrient concentrations. Under a dual relationship scenario (Fig. 3.1), if all lakes have high nutrient concentrations there should be a significant correlation between nutrients and turbidity. There was no significant correlation between nutrients and chlorophyll *a*, as would be expected under a nutrient-driven alternate regimes model. The correlation between TP and turbidity was most likely due to TP associated with resuspended sediments.

Nutrients did not drive turbidity across all study lakes because turbidity was dominated by phytoplankton in only eight of the 20 lakes (Fig. 3.5). Under an alternate, macrophyte-dominated clear and phytoplankton-dominated turbid regime model one would expect some sediment resuspension to contribute to turbidity as phytoplankton concentrations increase and reduce light available for macrophyte growth (Scheffer *et al.*, 1993). However, in this study, TSS was dominated by inorganic matter even in lakes with low turbidity values (<6 NTU). It is possible that some environmental factor other than nutrients limited macrophyte and phytoplankton productivity in some of the lakes, resulting in high proportions of inorganic TSS. For example, low light conditions (Blindow, 1992) and high nitrate concentrations (Lambert *et al.*, 2011), water movement and temperature (Bornette and Puijalon, 2011) may limit macrophyte growth. Many of the study lakes had high salinity (up to 41 g/L) and salt concentration has been shown to affect macrophyte productivity and diversity (e.g. Sim *et al.*, 2006b); Hammer *et al.*, 1988) and phytoplankton diversity (Hammer *et al.*, 1983). Charophytes are among the

most common macrophyte species in the study lake region and multiple charophyte species are unable to regulate vacuolar turgor at increasing salinities (Hart *et al.*, 1991). For example, *Chara corallina* can die within a day when exposed to 2.9 g/L NaCl because it cannot regulate turgor (Bisson and Bartholomew, 1984). Many of the lakes where TSS was dominated by inorganic matter had little or no macrophyte growth and all had salinities > 3 g/L (personal observation). The mechanism behind reduced macrophyte growth was not explored in these lakes, but it appears possible that the mechanism could be related to salinity. If salinity did inhibit macrophyte growth in the lakes, it likely contributed to the high inorganic content of TSS since rooted macrophytes were not present to stabilize the sediments (Scheffer, 1998).

The high proportions of inorganic turbidity in lakes of southern Alberta are not consistent with a key assumption in the phytoplankton-dominated turbid versus macrophyte-dominated clear model. Evidence over the past 20 years indicates that multiple additional shallow lake regimes may be possible (Scheffer and van Nes, 2007). Turbid waterbodies dominated by abiotic sources are also common in Australian surface waters (Strehlow *et al.*, 2005) and Australian wetlands have been observed in a clear regime dominated by benthic microalgae rather than macrophytes (Sim *et al.*, 2006c). McGowan *et al.* (2005b) also found evidence of a clear state characterized by benthic microbes in the Denmark. Others have found clear lakes dominated by floating-leaved plants (O'Farrell *et al.*, 2009) or by no macrophytes (Bayley *et al.*, 2007). If it is more appropriate to view lakes of southern Alberta in terms of three or more alternate regimes, correlations between nutrients and either turbidity or chlorophyll *a* cannot be expected within the high nutrient concentration range. It may be more likely to observe two

relationships at high nutrient concentrations; for example, one inorganic turbidity and one chlorophyll *a* relationship. Testing for multiple correlations would require a larger sample than the 20 lakes used in this study.

Jumps in time series

There was paleolimnological evidence of most lakes moving toward a more turbid state over time. All lakes but Brushy showed a progressive increase in phytoplankton abundance over time, suggesting possible landscape-level controls over eutrophication. Changes in five of the eight lakes appeared to be consistent with changes that would be expected for regime shifts. However, it is not possible to determine whether these lakes underwent relatively sudden shifts as would be expected under the alternate regimes model. The changes in all five lakes appear to be due to internal processes due to the asynchrony in their timing, rather than a regional driver.

Three criteria are used here to identify a jump in time series using sediment core proxies. First, there must be a change in sediment proxy abundance or concentration. Second, the sediment proxies must all be changing in the direction of either increased clarity or increased turbidity. Last, the change must be a “jump”, which is interpreted here as a noticeably sudden change compared to other time periods represented in the sediment core. Satisfying these three criteria does not provide conclusive evidence that a regime shift has occurred (Scheffer and Carpenter, 2003), but it does indicate that a shift may have occurred in a lake.

All eight lakes showed changes in sediment proxies. Most lakes also showed proxy trends that would be expected for lakes that are becoming more turbid over time;

declines in oospore concentration, $\delta^{13}\text{C}$ and C/N with concomitant increases in proxies for phytoplankton (lutein/zeaxanthin) and total plants and algae (β -carotene). Fresnell and Brushy lakes are the exceptions to these trends. In Fresnell Lake declines in $\delta^{13}\text{C}$ and C/N and increases in β -carotene were accompanied by a slight increase in lutein/zeaxanthin concentrations and the appearance of oospores in the most recent sediments, suggesting increased productivity overall rather than a trend toward turbid conditions. Long-term fluctuations in algal pigments in Brushy Lake differed from changes observed in other cores. In most recent sediments, there was a general increase in β -carotene (total plants and algae) accompanied by a decline in lutein/zeaxanthin (cyanobacteria and green algae) that suggests a transition from pelagic to benthic algae in the lake similar to that described for some lakes in Denmark (McGowan *et al.*, 2005b) and Australia (Davis *et al.*, 2010). Field sampling in August, 2007 confirmed that the lake bottom was covered in benthic algae but it was also extremely turbid, with very high concentrations of cyanobacteria and *Euglena sp.* (personal observation). Declines in the C/N ratio and $\delta^{13}\text{C}$ also suggests that algal production increased over recent years. Overall, it appears that Brushy Lake has been turbid due to abundant phytoplankton since 1850 and that there may have been more recent increase in phytoplankton-dominated turbidity.

The time series jump in the F3 core resembles a transition from a terrestrial environment to a lacustrine environment, even though the proxy trends were similar to those expected for a shift between clear and turbid regimes. Total plant and algae (β -carotene) pigment concentrations were extremely low prior to the cluster break, there were no oospores in the early sediments and C/N values corresponded to values associated with terrestrial plants. Most native grasses in the area (primarily *Bouteloua*

gracilis) used the C₄ photosynthetic pathway (Adams *et al.*, 2004) and would have produced $\delta^{13}\text{C}$ between -9 and -16 ‰ (Street-Perrott *et al.*, 1997) - similar to the values found in the F3 sediment record immediately preceding the time series jump. More recent sediments had more negative $\delta^{13}\text{C}$ values, as would be expected from freshwater phytoplankton (Cohen, 2003).

The clustering approach helped identify the time periods within each core where sediment proxies underwent relatively sudden changes. To satisfy the third criterion, these changes need to be noticeably sudden. The third criterion is more subjective than the first two and its interpretation was made more challenging by poor temporal resolution of some of the cores. Therefore, a liberal approach was taken to identify lakes that could have undergone a regime shift over time rather than to identify only the lakes that show very strong evidence of a sudden shift over time.

It is possible that a shift from a turbid to a clear regime could have occurred in all five remaining lakes. Temporal resolution is relatively fine in Hilton Long (seven years) and Hilton West (six years) lakes surrounding the cluster breaks, indicating that regime change occurred in a relatively short time. In Blackbird, Bland and Mushroom lakes, the temporal resolution surrounding the cluster breaks ranges from 38 - 41 years, which makes it impossible to determine whether increases in turbidity were gradual changes or rapid shifts.

Conclusion

There are several potential explanations why the shallow lakes of southern Alberta may not fit an alternate regimes model for shallow lakes. First, nutrient

concentration was the only control variable tested. Because phytoplankton does not dominate turbidity across all 20 lakes in this study, nutrients do not control turbidity across all of the lakes. Other control factors, such as water level (McGowan *et al.*, 2005a), light (Cymbola *et al.*, 2008), desiccation or freezing (Bayley *et al.*, 2007) planktivory (Carpenter and Kitchell, 1988) and macrophyte diversity (Sayer *et al.*, 2010) likely contribute to water clarity in these lakes. Future work could investigate each of these factors, rather than nutrients, as possible drivers of clear or turbid lake regimes.

Second, “space for time” analyses were used to examine bimodal distribution as an indicator of dual relationships between nutrients and turbidity. This approach assumed that a single control factor was the primary driver of turbidity across all lakes. In reality, a blend of controls impacted water quality in each lake (Scheffer and Carpenter, 2003), and the dominant control may have differed across lakes. For example, turbidity in some lakes may have been driven primarily by nutrients while climate or biotic interactions may have been more important in others. Since lakes existed over a range of turbidity values, it is certainly true that a single external driver was not the dominant control of turbidity for all lakes. While all internal controls could not be examined, the data do suggest that turbidity in some lakes is likely nutrient driven while in other lakes sediment resuspension, light limitation and zooplankton grazing are probably more important. Further data collection and analyses would be required to test this hypothesis.

Third, it is possible that these lakes spend more time in transition between clear and turbid regimes than would be expected under an alternate regime model. Sediment core analyses showed that seven of eight lakes studied grew more abundant in phytoplankton over time (the eighth lake had abundant phytoplankton throughout the

1800s and 1900s). However, it is possible that phytoplankton abundance increased gradually in many of the lakes, consistent with general eutrophication but not necessarily a turbid “attractor”. Lakes that are continually exposed to disturbances may spend more time in transition than under a single regime (Scheffer and van Nes, 2007). For example, Bayley *et al.* (2007) found that harsh winters in northern Alberta promoted thick ice cover and anoxia in very shallow lakes and that such conditions led to winterkill that essentially “reset” biological communities each year. Shallow lakes in southern Alberta also experience harsh winters that may annually interrupt their progression toward a relatively stable clear or turbid regime. Several of the lakes studied have been internally spatially heterogeneous over the past 10 years (unpublished data). Spatial heterogeneity may be another factor that increases the likelihood that lakes undergo gradual, rather than abrupt, transitions between regimes (van Nes and Scheffer 2005). Lakes in southern Alberta have low macrophyte species diversity relative to lakes in other Canadian provinces (L. Jackson, pers. comm.) and Sayer *et al.* (2010) observed a gradual reduction in macrophyte diversity over several years associated with increasing turbidity in European lakes. They suggested that lower macrophyte diversity provided opportunities through the growing season (temporal heterogeneity) for phytoplankton to establish, bloom and further compete with macrophytes.

Finally, it is possible that sediment cores from these shallow, polymictic lakes, do not exhibit sufficient spatial resolution down the core to identify abrupt changes. For example, Davidson *et al.* (2005) compared data from historical and sedimentary records for a shallow lake in England and observed that changes in community composition appeared less abrupt from the sedimentary record compared to historical data. While the

authors suggested that the discrepancy may have been due to gaps in the historical data, it is also plausible that the sedimentary record is less sensitive to abrupt changes due to mixing that time-averages deposits. This can occur through bioturbation prior to sampling or it can be an artefact of analytical techniques where sediments from a wide time span are analyzed within a single sample or mixed for some other reason (Cohen, 2003). Some of the sediment cores used in this research were taken from lakes with very low sedimentation rates leading to poor resolution and making them vulnerable to time-averaging during analysis and *in situ*.

CHAPTER FOUR: SALINITY EFFECTS ON TURBIDITY AND IMPLICATIONS FOR ALTERNATE REGIME MODELS

Introduction

Salinization of agricultural lands is a growing global problem (Gordon *et al.*, 2008) that has already impacted agricultural water bodies in arid and semi-arid regions (Williams, 2001). Naturally saline lakes exist, yet agricultural practices such as irrigation and land conversion from deep rooted plants to shallow rooted pasture and crops contribute to extensive secondary salinization. Salinity increases alter biological communities, reduce biodiversity and change natural hydrologic patterns (Williams, 2002).

Much of the semi-arid prairie of southern Alberta was converted to agriculture following the late 1800s and, since 1950, there has been an increase in visible salinity on Alberta's agricultural lands (Cannon and Wentz, 2000). Anticipated increases in average annual temperature for the Calgary area range from ~2-8 °C by 2080 with only 20-50 mm of additional annual precipitation (Barrow and Yu, 2005). Increased temperatures with little additional precipitation will likely lead to greater moisture deficits and increased salinization. The prairies of Canada and the northern United States are covered with hundreds of thousands to ten million pothole lakes and wetlands (Covich *et al.*, 1997; Last and Ginn, 2005). Small lakes and wetlands are important sources of biodiversity in agricultural landscapes (Søndergaard *et al.*, 2005) and are important breeding habitat for migratory waterfowl in southern Alberta. Groundwater is an important contributor to annual water budgets in Alberta's pothole lakes, yet salinity in the lakes is also affected

by high evaporation: precipitation ratios (Covich *et al.*, 1997). Southern Alberta's lakes range from fresh (TDS < 500 mg/L) to highly saline (e.g. TDS > 50 000 mg/L) due to the combined effects of agricultural salinization of groundwater and high evaporation: precipitation ratios. Salinity impacts may become increasingly pronounced in the future as the past century has been uncharacteristically wet (Laird *et al.*, 2003).

Water's salinity characteristics shape aquatic communities. Aquatic organisms experience osmotic stress when the concentration of total dissolved solids (TDS) is high. Halo-tolerant species employ strategies such as altering intracellular concentrations of amino acids (Saros and Fritz, 2000) or other osmolytes (Hart *et al.*, 1991) that alter internal osmotic pressure. Other organisms are simply replaced by halo-tolerant species as salt concentrations extend beyond their tolerance ranges. In shallow lakes like those found in southern Alberta, organisms may also be subjected to large fluctuations in TDS over a summer resulting in community composition changes or communities dominated by organisms with wide salinity tolerance. The ion composition of salts also affects aquatic community composition. For example, high concentrations of sulphate may interfere with nitrogen fixation and the prevalence of nitrogen fixing cyanobacteria (Marino *et al.* 2003). While some diatoms are favoured in water dominated by sulphate, other diatoms are favoured in water with high bicarbonate concentrations (Saros and Fritz, 2000). Sulphate and iron influence phosphorus cycling (Caraco *et al.* 1989; Clavero *et al.*, 1990; Jordan *et al.*, 2008) and metal cations such as magnesium can reduce phosphorus bioavailability through competitive binding (Waiser and Robarts, 1995).

Nutrient controls over phytoplankton abundance have been well studied (e.g. Dillon and Rigler, 1974; Schindler, 1978), but general nutrient models do not predict

phytoplankton biomass in all lakes. Saline lakes are typically less productive than would be expected under classic nutrient-phytoplankton models (e.g. Bierhuizen and Prepas, 1985; Evans and Prepas, 1996; Håkanson and Eklund, 2010). Alternate regime models developed for shallow, polymictic lakes in northern Europe suggest a more complex relationship between nutrients and phytoplankton biomass (Scheffer *et al.*, 1993) where over an intermediate range of nutrient concentrations some lakes can exhibit either very high or relatively low phytoplankton abundance due to positive feedbacks that maintain the lakes in turbid or clear regimes, respectively (Fig. 4.1). Lakes are maintained in a turbid, phytoplankton-dominated regime when shading reduces macrophyte biomass, there is low competition for nutrients and grazing pressure from zooplankton is low. Clear, submerged macrophyte-dominated lakes are possible when water is shallow and allows light to penetrate to the bottom. Submerged macrophytes that establish early in the season avoid light competition from phytoplankton and the macrophytes compete for nutrients and provide refugia for large zooplankton that most effectively graze phytoplankton. Macrophytes also anchor lake sediments and reduce turbidity due to sediment resuspension. Some studies have found evidence of these alternate regimes in shallow lakes (e.g. Scheffer *et al.*, 1993; Jackson 2003; Zimmer *et al.*, 2009), yet others have not (e.g. Bayley and Prather, 2003; McGowan *et al.*, 2005b; Sim *et al.*, 2006a; Bayley *et al.*, 2007).

The purpose of this research was to determine how salt concentration and ion composition affect phytoplankton-dominated turbidity in the lakes of southern Alberta and whether these effects help explain why some shallow lakes in southern Alberta do not fit the alternate regimes model for shallow lakes (Scheffer *et al.*, 1993). Because high

salt concentrations are often associated with lower phytoplankton biomass, the hypothesis was that either total salt concentration or concentrations of particular major ions would be associated with low turbidity, even under high nutrient conditions. Several objectives were met to investigate this hypothesis. The first objective was to verify that phytoplankton biomass was low in lakes with high salt or major ion concentrations and were not related to nutrient concentrations. The second objective was to determine whether total turbidity was low in lakes with high salt concentration and was not related to nutrient concentrations. The third objective was to determine whether high sulphate concentrations were related to low abundance of heterocystous cyanobacteria, as would be expected based on Marino *et al.* (2003). A modified version of the alternate regimes model for shallow lakes (Scheffer *et al.*, 1993) may better describe saline prairie lakes if salt concentration and ion composition do affect phytoplankton biomass.

Methods

Study area

Twenty shallow lakes were sampled in the mixedgrass ecoregion of southern Alberta's prairie (Strong 1992), within 125 km of Strathmore (Fig. 4.2). The region is dominated by dark brown or black Chernozemic soil. The region was grazed by bison (*Bison bison bison*) historically and, since European settlement in the mid-late 19th century, has been primarily used as agricultural land. Wheat, barley and canola have been the primary crops in the area for at least the past 50 years while cattle ranching and pork production have been the primary livestock operations over the same time (Statistics Canada 1966-2006).

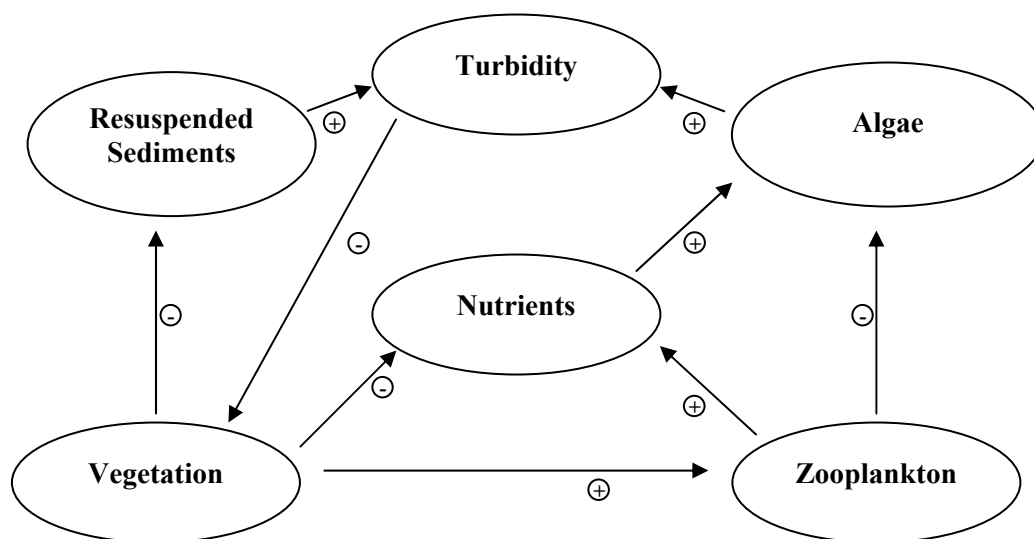


Figure 4.1. Conceptual model (modified from Scheffer *et al.*, 1993). The model shows the main feedback loops that maintain shallow lakes under clear or turbid regimes. Clear regimes are dominated by macrophytes (vegetation). Macrophytes anchor sediments, consume nutrients and provide refugia for large zooplankton that graze phytoplankton. These mechanisms promote water clarity that supports macrophyte photosynthesis and production. Turbid regimes are dominated by phytoplankton (algae). Phytoplankton and suspended sediments increase turbidity and reduce macrophyte photosynthesis and biomass. Lower macrophyte biomass results in less sediment anchoring, greater nutrient availability to phytoplankton and fewer large-bodied zooplankton that graze phytoplankton. Consequently low macrophyte biomass enhances turbidity through increased sediment resuspension and higher phytoplankton production.

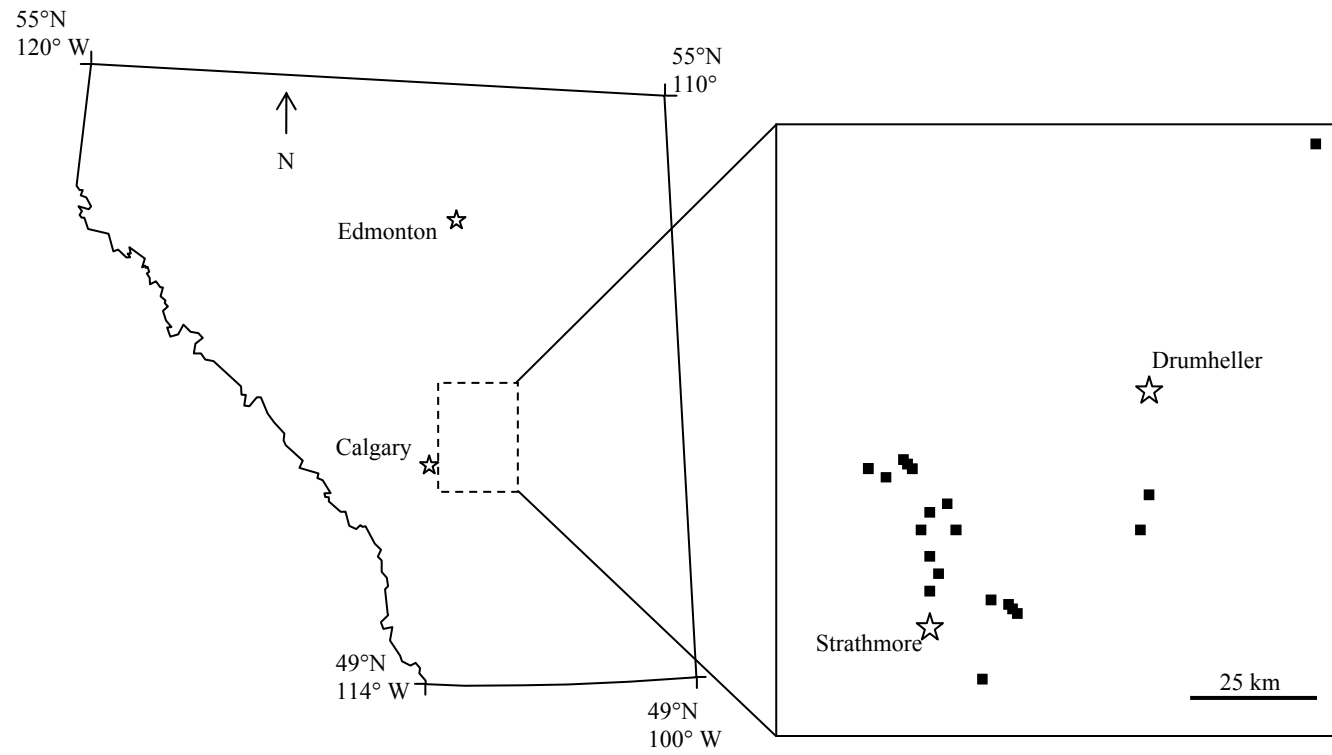


Figure 4.2. Location of 20 shallow, prairie lakes sampled in southern Alberta (black squares) to determine how salinity affects phytoplankton.

Shallow lakes are defined here as permanent, lentic water bodies. The 20 shallow lakes sampled are small (< 40 ha, mean = 7 ha), shallow (depth ≤ 2.7 m, mean = 1.0 m) and polymictic (Table 4.1). They range in salt concentration from fresh (< 0.5 g/L) to highly saline (41.3 g/L). Salt composition is variable, but tends to be dominated by sodium, sulphate and/or bicarbonate. The lakes sampled are closed systems, with major inputs being snowmelt and groundwater and primary loss occurring through evaporation. There are no piscivores in the systems and brook stickleback (*Culaea inconstans*), where they occur, are the main planktivores.

Some analyses were supplemented with additional lakes from a broader geographic area (located within 400 km of Strathmore) including the foothills fescue and dry mixed grass regions dominated by agriculture. The additional lake data were drawn from Alberta Environment open files and were added to increase sample size and attempt to generalize results from shallow to deep lakes.

Field and laboratory methods

Water samples were collected from the 20 lakes during the last two weeks of August, 2007 to quantify water chemistry and phytoplankton community composition. All samples were collected from the centre of each lake directly from the water column at a 0.5 m depth, except where $Z_{\max} < 0.5$ m in which case samples were taken from mid-depth. Samples for phytoplankton enumeration and alkalinity were collected in 240 ml glass bottles. Phytoplankton samples were filled leaving ~ 10 ml air space and preserved immediately with several drops of Lugol's iodine solution. Two additional phytoplankton samples were collected at randomly selected sites at either end of each lake. Bottles that

Table 4.1. Lake location and selected chemical and biological characteristics of 20 shallow, prairie lakes in southern Alberta.

Lake	Location	Surface Area (ha)	Z _{max} (m)	TDS (mg L ⁻¹)	Turbidity (NTU)	TP (µg L ⁻¹)	TN (µg L ⁻¹)	TN: TP	Chl _a (µg L ⁻¹)	pH	Total Alkalinity (mg CaCO ₃ L ⁻¹)	Heterocystous Cyanobacteria (%)
Mushroom	51°06': 113°24'	11.7	1.3	626	4.1	69	2,263	33	4.7	11.3	302	< 0.1
Bland	51°15': 113°21'	9.2	1.2	644	20.6	1,152	2,094	2	44.1	9.8	287	< 0.1
Carlson	51°12': 113°01'	11.5	1.7	666	3.8	30	1,300	44	5.0	9.2	238	<1.0
HWest	51°03': 113°11'	3.6	1.8	1,100	40.6	270	2,080	8	96.3	9.8	312	70.6
HEast	51°03': 113°11'	3.5	1.4	1,215	34.8	244	1,819	7	65.9	9.7	333	40.8
HLong	51°03': 113°11'	9.5	1.6	1,538	53.6	234	3,396	14	97.8	9.9	361	75.6
Barnett	51°04': 113°14'	27.7	2.1	2,972	1.1	16	1,378	85	1.1	9.3	627	<1.0
Cattleland	51°00': 113°23'	14.2	1.15	3,365	59.7	9,391	11,720	1	27.1	9.2	745	< 0.1
Salty Pond	51°17': 113°02'	0.9	0.4	4,661	17.5	7,605	6,443	1	0.9	10.2	1,583	<1.0
Blyth	50°56': 113°15'	3.9	0.25	5,260	96.0	3,935	3,923	1	6.0	9.8	1,323	<1.0
Rose	51°15': 112°46'	5.4	1.85	5,288	5.6	35	2,548	74	0.9	9.3	562	< 0.1
Fresnell 3	51°01': 113°02'	0.5	1.07	5,542	4.5	606	6,443	11	1.5	10.1	2,027	<1.0
Fresnell 4	51°01': 113°34'	8.7	0.29	5,864	11.8	3,878	4,367	1	11.0	9.4	429	< 0.1
Long #2	51°12': 113°25'	32.5	0.4	6,755	340.0	17,269	2,683	0.2	17.5	10.2	3,056	0
Libellule	51°52': 112°16'	13.8	0.1	7,250	178.3	8,565	2,946	0.3	1.5	10.2	2,284	0
Dawson	51°08': 113°20'	31.4	1.7	7,499	19.1	463	4,438	10	1.8	9.7	1,066	<1.0
B.Fresnell	51°01': 113°02'	0.4	0.25	16,746	61.6	4,790	9,662	2	16.2	10.5	3,432	0
Blackbird	50°11': 112°47'	3.6	0.45	17,761	18.7	1,641	5,757	4	6.5	9.7	832	< 0.1
Fresnell	51°01': 113°02'	2.1	1.0	32,430	66.0	3,890	11,430	3	17.7	10.5	4,702	<1.0
Brushy	51°14': 113°24'	31.4	0.7	41,289	135.0	10,217	26,420	3	246.5	11.0	24,376	78.9

contained water for alkalinity determination were filled to the top and closed underwater using air-tight caps to ensure no air bubbles were present within the samples. The remaining water samples were collected with 1 L Nalgene® bottles at 0.5 m depth (mid-depth if $Z_{\max} < 0.5$ m) directly from the water column. Bottles used to collect samples for ion analyses were washed and rinsed at least seven times with de-ionized water. Bottles for the remaining water samples were washed, acid-bathed and then rinsed with distilled water. All samples were kept on ice in dark coolers until they reached the lab.

Temperature, conductivity, dissolved oxygen and pH were all measured directly in the field in the centre of each lake at 0.5 m depth (mid-depth if $Z_{\max} < 0.5$ m) using a Hydrolab mini-sonde equipped with a Surveyor 4 data logger. Nephelometric turbidity was measured using an Orbeco-Hellige (model 966) portable turbidity meter.

Chlorophyll *a* and nutrient samples were analysed or preserved within 24 hours of sampling to avoid degradation. Chlorophyll *a* samples (between 25-350 ml per sample) were filtered through Whatman GF/C filters under minimal light. Chlorophyll *a* was extracted into acetone following Strickland and Parsons (1968) and quantified fluorometrically with correction for phaeopigments. Total nitrogen (TN) and total carbon (TC) samples were refrigerated (4 °C) immediately and then analyzed with ion chromatography (Dionex ICS-1000 Ion Chromatography System) within 28 days of collection. Total phosphorus (TP) and soluble reactive phosphorus (SRP) were analysed within 24 hours using the molybdate blue method (Strickland and Parsons, 1968).

Total suspended solids (TSS) were measured to quantify lake turbidity composition. Between 250-1250 ml of water were filtered over pre-weighed and labelled

GF/F filters, dried to constant mass at 60 °C and then weighed to determine weight of suspended solids. Organic matter was determined as loss on ignition at 550 °C.

Major anions and cations were measured to assess salinity, defined as total dissolved solids (TDS), and relative ion composition for each lake. Cation samples were filtered through a 0.45 µm syringe filter and acidified with HNO₃ to pH < 2 then refrigerated (4 °C). Sodium, potassium and calcium concentrations were analysed using ion chromatography (Dionex ICS-1000 Ion Chromatography System) while magnesium concentrations were measured by atomic absorption spectrophotometry (Perkin-Elmer AAnalyst 100). Alkalinity, sulphate, and chloride samples were refrigerated until analysis by ion chromatography. Nitrate and nitrite samples were acidified with H₂SO₄ to pH < 2 prior to refrigeration and then measured using continuous flow analysis (CFA) in a Technicon AutoAnalyzer. Carbonate and bicarbonate were calculated from titration endpoints that were measured using an Orion Autochemistry 960 Autotitrator. All ion samples were analyzed within 28 days of collection.

Phytoplankton were counted following the methods outlined in Findlay and Kling (2003) and identified to species, when possible, using Wehr and Sheath (2003).

Phytoplankton biomass (mg/L) was calculated for each freshwater algal division and separately for heterocystous cyanobacteria in each of the 60 samples.

Expanded data set

Additional data collected by Alberta Environment from 17 deep and shallow lakes were used to increase sample size to 37 lakes and to test the generality of our findings across a broader geographic region and range of lake depths (Appendix C).

Chlorophyll *a*, TP, TN and TDS data were taken from Alberta Environment open files

[<http://envext02.env.gov.ab.ca/crystal/aenv/viewreport.csp?RName=Detailed%20Lake%20Water%20Quality%20Data>].

Statistical analyses

All statistical analyses were performed using the R language and software environment (Version 2.10; R Development Core Team, 2010). Correlations, rather than regressions, were used to relate variables to each other to avoid the assumption of causal linkages among variables. Pearson's product moment correlation was used when the data were bivariate normal; otherwise, Spearman's rank correlations were used.

Welch's approximate t-test was used to compare mean chlorophyll *a* and mean chlorophyll *a*: nutrient ratios between low and high salinity lakes because the data did not have equal variances. The sample sizes were small, making it difficult to determine if the variables were normally distributed. Data transformations did not help. T-tests were repeated using randomization (10,000 runs) to generate a null distribution for the data from which p-values were calculated. Permutation results were similar to those of Welch's approximate t-tests.

Results

Phytoplankton biomass

Spearman's rank correlations across the 20 lakes did not reveal any significant relationships between chlorophyll *a* and TP, TN or SRP (Table 4.2). Chlorophyll *a* concentrations were not significantly higher ($p = 0.28$, $df = 14.5$) in lakes where $TDS < 2.5$ g/L, a concentration above which nitrogen-fixation may be impaired (Evans and

Table 4.2. Correlation coefficients and associated significance for turbidity, TDS, TSS and chlorophyll *a* with TDS, TSS, chlorophyll *a*, %TSS_{organic} TN and TP.

	TDS	Turbidity	TSS	Chlorophyll <i>a</i>
Turbidity	0.47*			
TSS	0.63**	0.83***		
Chlorophyll <i>a</i>	-0.027	0.52*	0.37	
% TSS _{organic}	-0.85*** ¹	-0.35		
TN	0.72***	0.41	0.48*	0.12
TP	0.58**	0.77***	0.71**	0.22
SRP				-0.083

Significance levels (p values) are indicated as follows: <0.001 by ***, <0.01 by **, and <0.05 by *.

¹The correlation between % TSS_{organic} and TDS was restricted to TDS between 0-10 mg/L (n=16).

Prepas, 1996), (mean = 32.0 $\mu\text{g/L}$ Chl *a*) compared to those with higher TDS (mean = 21.5 $\mu\text{g/L}$ Chl *a*) (Fig. 4.3a). Lakes with higher salt concentrations generally had low chlorophyll *a* concentrations, yet Brushy Lake had an extreme chlorophyll *a* concentration and very high salinity which resulted in the insignificant difference in mean chlorophyll *a* between the high and low salinity lakes. Chlorophyll *a* concentrations were consistently low when sulphate or magnesium concentrations were high (Fig. 4.4).

Chlorophyll *a*: nutrient ratios showed an asymptotic relationship with salinity where the ratio was consistently low at salinities greater than 2.5 g/L (Fig. 4.3), even with Brushy Lake. Welch's approximate t-tests indicated that mean chlorophyll *a*/TP ($p = 0.021$, $df = 5.06$) and mean chlorophyll *a*/TN ($p = 0.033$, $df = 5.10$) were significantly higher in the 6 lakes with $\text{TDS} < 2.5$ g/L compared to the 14 lakes where $\text{TDS} > 2.5$ g/L. The mean chlorophyll *a*/SRP ratio was not significantly different ($p = 0.0088$, $df = 5$) between high and low salinity lakes, but the chlorophyll *a*/SRP ratio was consistently low in the high salinity lakes (Fig. 4.3) and there were several low salinity lakes with high chlorophyll *a*/SRP ratios.

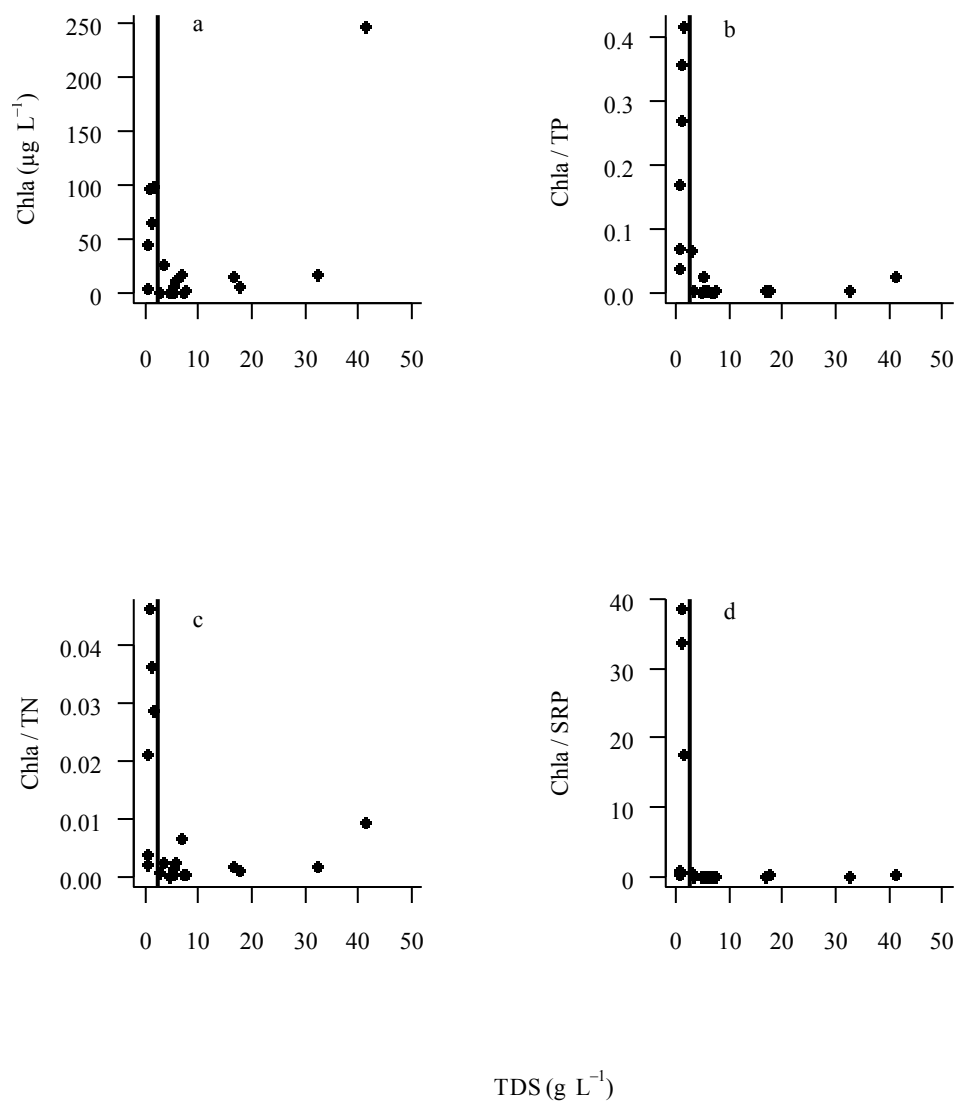


Figure 4.3. Relationships between TDS and chlorophyll *a* (a), TDS and chlorophyll *a* /TP (b), TDS and chlorophyll *a* /TN (c) and TDS and chlorophyll *a* /SRP (d). Water samples were taken from the 20 shallow lakes in southern Alberta in August, 2007. Bars indicate TDS = 2.5 g /L and represent the concentration at which salinity has been hypothesized to impair nitrogen fixation (Evans and Prepas, 1996).

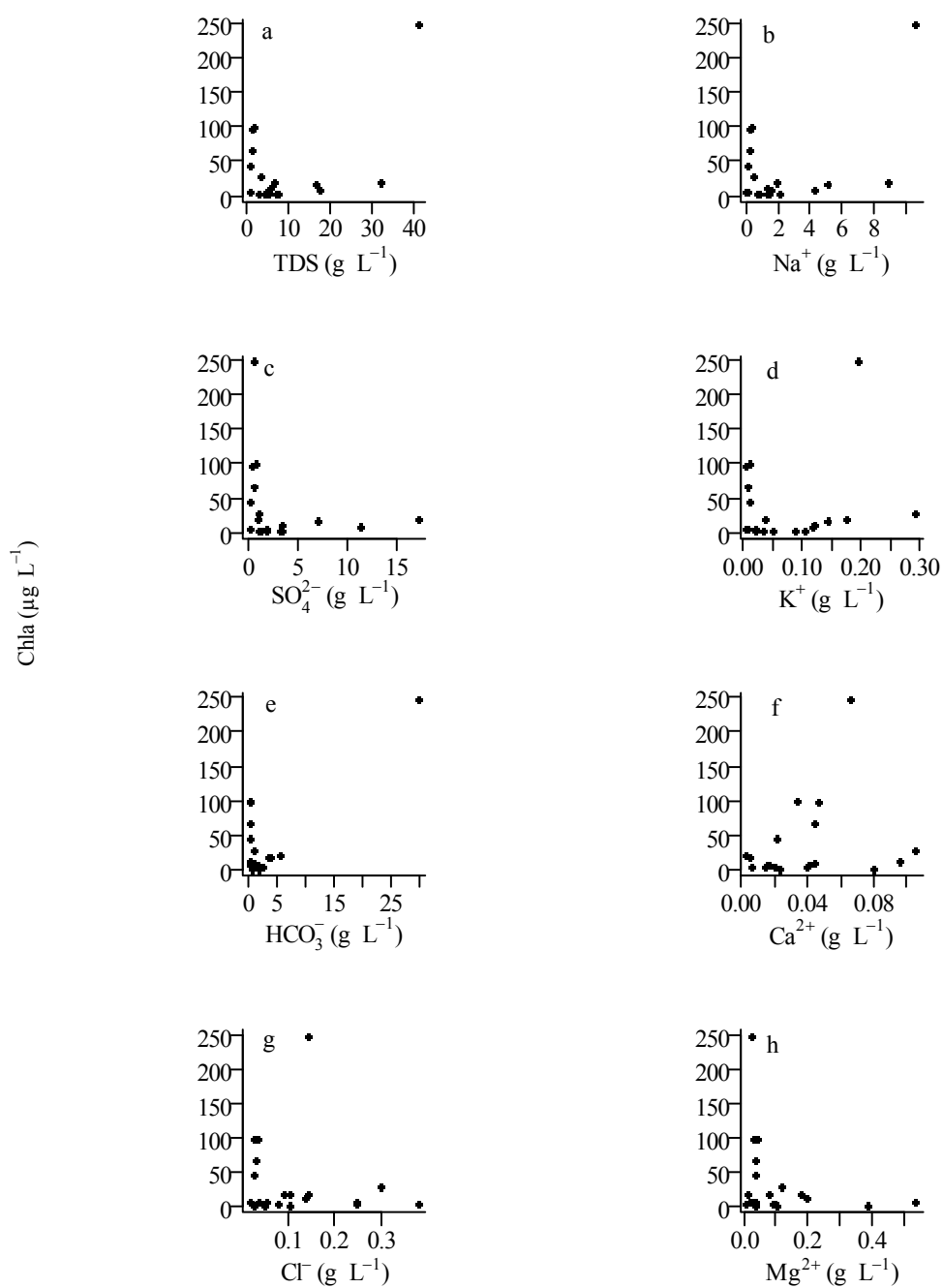


Figure 4.4. Relationships between TDS and chlorophyll a (a) and major ions and chlorophyll a (b-h) for water samples taken from 20 shallow lakes in southern Alberta in August, 2007.

Turbidity

Salinity was correlated with turbidity and total suspended solids (TSS) but not chlorophyll *a* concentration (Table 4.2, Fig. 4.5). Spearman's rank correlation identified a significant linear correlation between total dissolved solids (TDS) and turbidity across the 20 shallow study lakes. The correlation between TDS and TSS was stronger and more highly significant. There was no significant correlation between chlorophyll *a* and TDS or TSS. Chlorophyll *a* was significantly correlated with turbidity, yet the correlation was relatively weak.

Turbidity and TSS were significantly and strongly correlated (Table 4.2). The organic carbon content of TSS declined as salt concentrations increased to 10 g/L and then increased as TDS increased (Table 4.2, Fig. 4.6). The inverse correlation between % TSS_{organic} and TDS (0-10 g/L) was strong and highly significant. There was no significant correlation between % TSS_{organic} and turbidity. In lakes where TDS < 2.5 g/L (Fig. 4.6), chlorophyll *a* contributed more to TSS than in more saline lakes.

Spearman's rank correlation revealed a stronger relationship between TN and TDS than TP and TDS (Table 4.2). Correlations for TP with turbidity and TSS were stronger than the relationship between TP and TDS. The relationship between TN and TSS was significant but weaker than the relationship with TDS while the correlation between TN and turbidity was not significant.

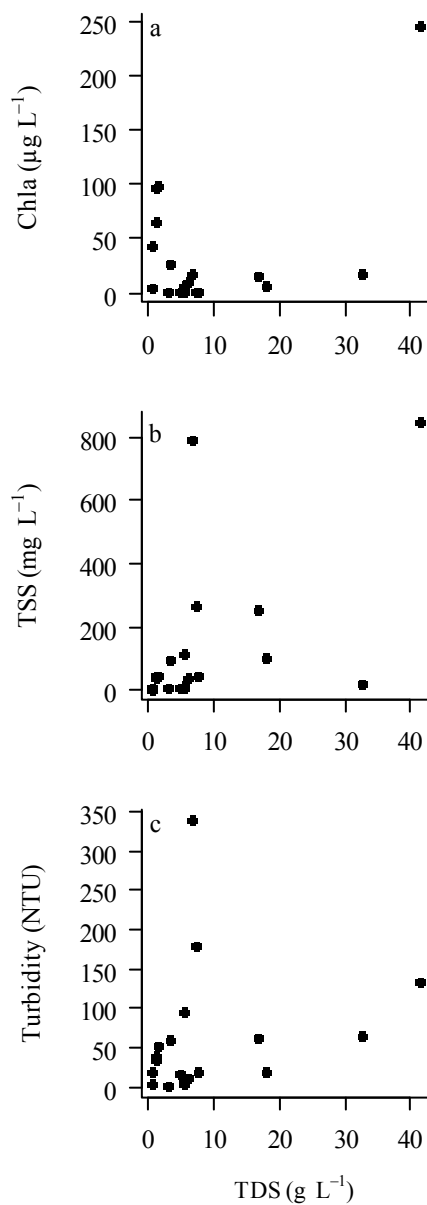


Figure 4.5. Relationships between total dissolved solids (TDS) and three measures of water clarity; chlorophyll *a* (a), total suspended solids (TSS) (b) and turbidity (c) for water samples taken from 20 shallow lakes in southern Alberta in August, 2007.

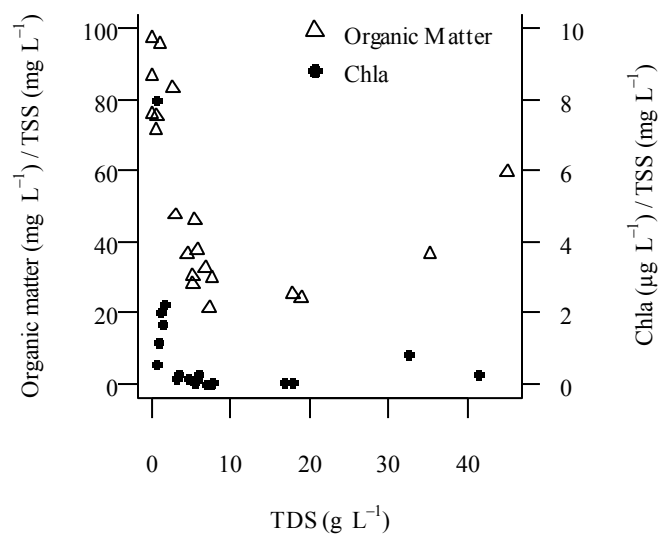


Figure 4.6. Changes in contributions of organic matter (left axis, open triangles) and chlorophyll *a* (right axis, closed circles) to TSS along a salinity gradient for water samples taken from 20 shallow lakes in southern Alberta in August, 2007.

Heterocystous cyanobacteria

Chlorophyll *a* concentrations were higher when heterocystous cyanobacteria were abundant. Heterocystous cyanobacteria were present in 17 of the 20 lakes, but comprised less than 6 % of the phytoplankton community biomass in 13 of those lakes. The remaining 4 lakes had very high proportions heterocystous cyanobacteria ranging from 41-79 % of the phytoplankton community biomass (Fig. 4.7). These lakes had the highest phytoplankton biomasses with chlorophyll *a* concentrations ranging from 98-246 µg/L while all other lakes contained less than 45 µg/L of chlorophyll *a*.

The proportion of nitrogen-fixing cyanobacteria was low (Fig. 4.8) when sulphate or magnesium concentrations were high. All other ions were present in moderate – high concentrations in at least one of the 4 lakes with high chlorophyll *a* concentrations and high proportions of heterocystous cyanobacteria. Heterocystous cyanobacteria comprised nearly 80 % of the phytoplankton biomass in Brushy Lake, the lake with the highest TDS (Fig. 4.8a) and chlorophyll *a* (Fig. 4.7).

Expanded data set

Data collected by Alberta Environment from 17 deep and shallow lakes were used to test correlations between total nutrients (TN, TP), salt concentrations (TDS) and chlorophyll *a* across a broader geographic region and range of lake depths (Appendix C). Results were similar to those obtained for the 20 shallow lakes, including significant correlations between total nutrients and TDS, no correlations between TP or TN and chlorophyll *a*, mean chlorophyll *a* concentrations were not significantly different between

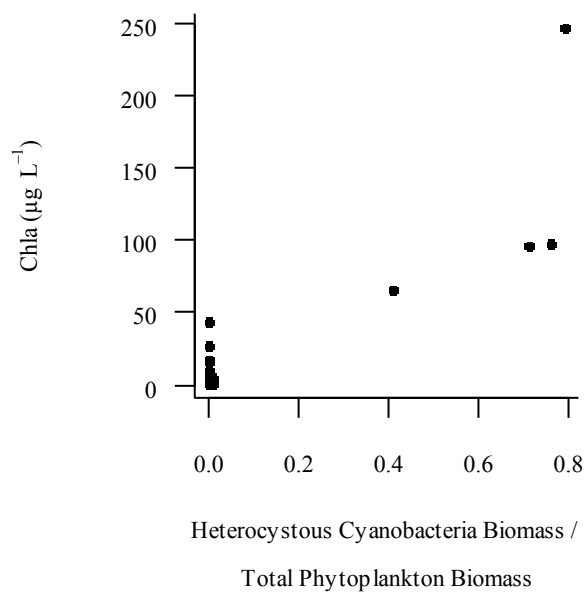


Figure 4.7. Relationship between chlorophyll *a* concentration and the proportion of heterocystous cyanobacteria contributing to total phytoplankton biomass from 20 shallow lakes in southern Alberta in August, 2007.

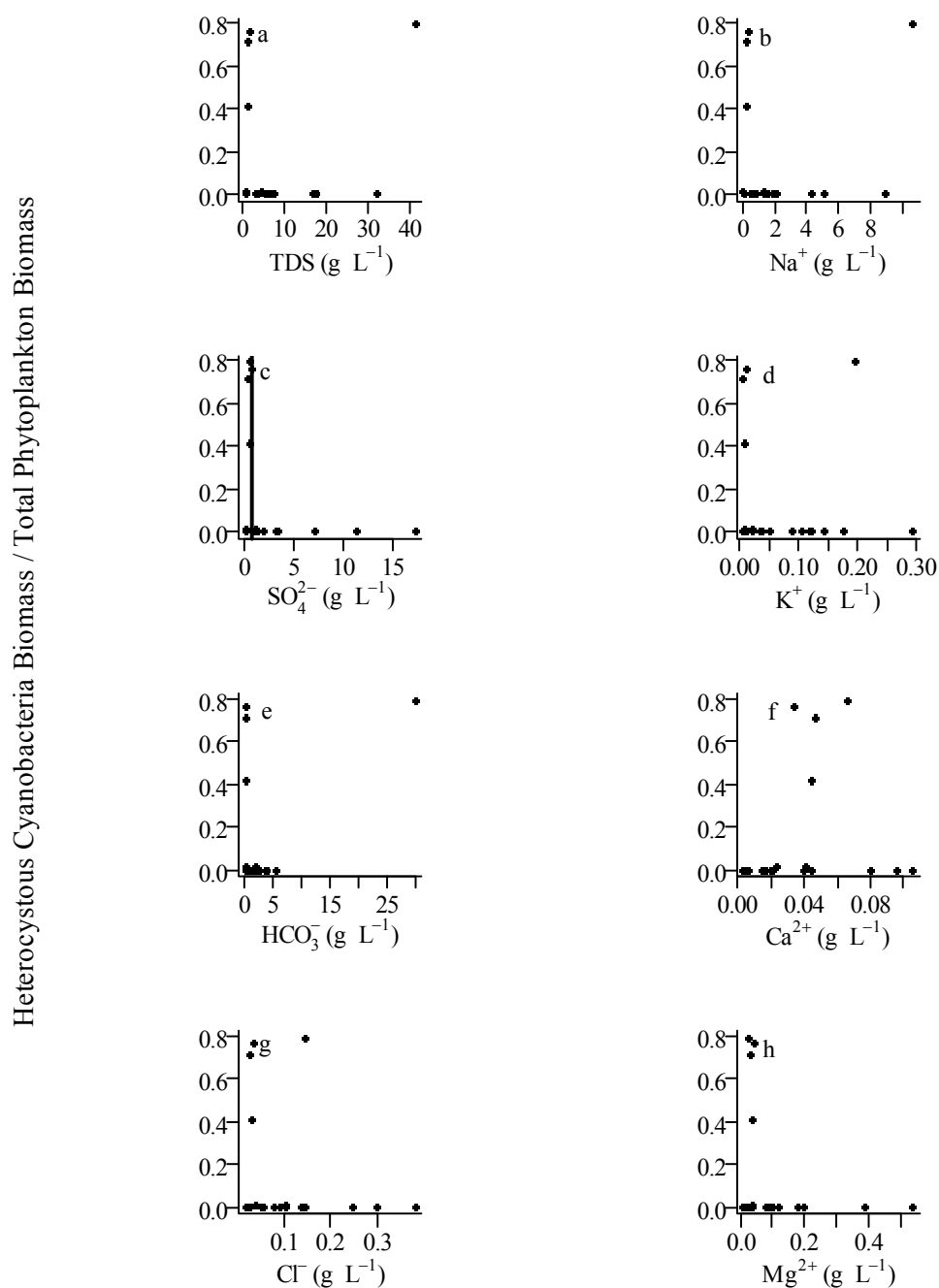


Figure 4.8. Relationships between TDS and the proportion of phytoplankton with nitrogen-fixing heterocysts (panel a) and major ions and proportion of phytoplankton with nitrogen-fixing heterocysts (panels b-h) for water samples taken from 20 shallow lakes in southern Alberta in August, 2007. The bar in panel c represents a sulphate concentration of approximately 768 mg/L (8 mM). Marino *et al.* found that molybdate assimilation and, therefore, nitrogen fixation, was inhibited at sulphate concentrations > 8 mM.

high and low salinity lakes and mean chlorophyll *a*/nutrient ratios were significantly higher in low salinity lakes.

Discussion

Phytoplankton abundance in a number of lakes sampled was affected by salt composition and ion concentrations, as expected (e.g. Bierhuizen and Prepas, 1985; Evans *et al.*, 1996; Evans and Prepas, 1997; Marino, 2003). Shallow lakes in southern Alberta differed from expectations of existing shallow lake models (Scheffer *et al.*, 1993) in two important ways: first, common nutrient-phytoplankton relationships did not exist and, second, phytoplankton was not consistently an important source of turbidity. Turbidity generally increased with salt concentration and was not due to water becoming “greener”. In fact, TN, TP nor SRP had significant relationships with phytoplankton abundance. As a result, not all Alberta shallow lakes fit turbidity models that have been developed for shallow lakes in northern Europe and have formed an important conceptual framework of alternate regimes in shallow lakes.

Data here show that high salinity was a key reason for differences between model expectations and turbidity patterns observed in shallow lakes from southern Alberta. One saline and three moderately saline lakes had chlorophyll *a* concentrations > 50 µg/L, low sulphate and magnesium concentrations and high proportions of heterocystous cyanobacteria. Numerous *in situ* experiments have demonstrated that heterocystous cyanobacteria are more likely to exist when dissolved inorganic nitrogen and urea are low (Barica *et al.*, 1980; Finaly *et al.*, 2010; Donald *et al.*, 2011), suggesting that phytoplankton in at least four lakes were nitrogen-limited, despite high TN

concentrations. This would be possible if only a fraction of the TN was biologically available. Phytoplankton biomass in some of the other sixteen shallow lakes may also be nitrogen-limited but, due to high sulphate concentrations which have been shown to inhibit nitrogen fixation (Marino *et al.*, 2003), were unable to use N₂. Therefore, a regional shallow lake turbidity model for southern Alberta, and likely a large area of the Great Northern Plains, should consider how salt concentration and composition influence phytoplankton biomass and should focus more on how suspended solids rather than phytoplankton impact water clarity.

Phytoplankton biomass

Phytoplankton biomass was not correlated with nutrient concentrations or TDS but was relatively low in most lakes with high TDS (Table 4.2, Fig. 4.3). These results are consistent with other field studies in western Canada that found no correlation between TN or TP and Chlorophyll *a* in saline lakes from southern Alberta with low N:P ratios (Bierhuizen and Prepas, 1985), similar to the ratios in this study. Evans *et al.* (1996) suggested that intense zooplankton grazing can depress phytoplankton biomass in saline lakes in Western Canada. In other saline prairie lakes alkalinity may reduce iron availability to phytoplankton (Evans and Prepas, 1997). In addition to total salinity, individual ions can depress phytoplankton biomass through variety of mechanisms, as described below. Of the major ions I measured, only sulphate and magnesium were associated with consistently low chlorophyll *a* concentrations and are known to affect nutrients availability (e.g. Cole *et al.*, 1986; Waisar and Robarts, 1995; Marino *et al.*, 2006).

Despite a general trend toward lower phytoplankton biomass at high salinity, mean chlorophyll *a* concentrations were not significantly lower for lakes placed in the high salinity (>2.5 g/L) group (Fig. 4.3). This was mainly due to Brushy Lake which had high TDS and chlorophyll *a* concentrations, but chlorophyll *a* values in the more saline lakes were not exceptionally low. Only five of the fourteen most saline lakes would be consider oligotrophic based on chlorophyll *a* concentrations.

Chlorophyll *a*/ nutrient ratios were used to assess how salinity might influence phytoplankton assimilation of N and P. At increasingly high TDS, phytoplankton biomass was lower per unit TN or TP, and TN and TP were poor predictors of phytoplankton biomass in the more saline lakes (TDS>2.5 g/L). Evans and Prepas (1996) also found lower than expected phytoplankton biomass when salinity increased beyond a similar salinity threshold (~3500 $\mu\text{S}/\text{cm}$) in 6 other Alberta lakes. However, my results here contradict expectations from a model recently developed to relate chlorophyll *a* values in saline systems to phosphorus and nitrogen (Håkanson and Eklund, 2010) that predicts a peak in chlorophyll *a*/ nutrient ratios as salinity reaches ~10 -15 g/L followed by a decline thereafter. My results indicate there is surplus TP and TN in the more saline lakes and this implies that less TP and/or TN is biologically available at high salinities or that something other than P and/or N is limiting phytoplankton biomass at high salinities.

For several decades phosphorus has been known to limit phytoplankton biomass (e.g. Vollenweider, 1976; Schindler, 1978; Schindler, 2006) but TP and SRP have been poor measures of phosphorus available for phytoplankton growth in saline prairie lakes (Waisar and Robarts, 1995). Though phosphorus concentrations were high across the study lakes, it is likely that not all of the phosphorus was biologically available. For

example, total phosphorus includes phosphorus that readily binds with metal cations such as Mg^{2+} and dissolved organic carbon (DOC), making such phosphorus unavailable for phytoplankton uptake (Waisar and Robarts, 1995). I did not measure DOC, yet Curtis and Prepas (1993) found high DOC in the saline lakes of central Alberta. Lakes I sampled that have high Mg^{2+} concentrations also have relatively low phytoplankton abundance, which could occur if Mg^{2+} limits phosphorus bioavailability.

Nitrogen can also limit phytoplankton biomass (e.g. Donald, *et al.*, 2011; Elser *et al.*, 2007) and, even under high nitrogen conditions, nitrogen deficiencies have been observed in other saline prairie lakes (e.g. Salm *et al.* 2009). The strongest evidence for nitrogen limitation in this study is the high proportion of heterocystous cyanobacteria in the four lakes with the highest phytoplankton concentrations. Because heterocyst production is energetically expensive, cyanobacteria should only produce heterocysts if biologically available nitrogen is limiting (Howarth *et al.*, 1988; Jensen *et al.*, 1994).

Alkalinity was especially high among the more saline lakes and it has been suggested that that relatively high alkalinities contribute to greater binding between ammonia and humic DOM, reducing ammonia bioavailability (Steinberg, 2003) in aquatic systems.

Ammonium ions also sorb strongly to minerals and the significant correlation between TSS and TDS coupled with the negative correlation between organic TSS and TDS implies that there was more suspended mineral available in the water column to which ammonium could sorb at high salinity.

There may also be barriers to assimilating biologically available nitrate which, as Österlind (1947) showed, is a more important nitrogen source than ammonia for phytoplankton growth at $\text{pH} > 9.5$. All lakes had $\text{pH} > 9$ and 15 of the shallow lakes had

pH > 9.5. Iron and molybdenum are essential for nitrate assimilation (Milligan and Harrison 2000). Evans and Prepas (1997) determined that iron availability was low in 11 saline lakes in central Alberta due to binding with particulates. High sulphate concentrations can reduce iron concentrations in the water column through binding and precipitation of iron sulphide (Jordan *et al.*, 2008) and may also inhibit assimilatory nitrate reduction by inhibiting molybdate uptake in phytoplankton (Cole *et al.*, 1986; Saros and Fritz, 2002).

Additional factors such as light limitation and zooplankton grazing could also affect phytoplankton biomass in the saline study lakes. Jeppesen *et al.* (2007) found an increase in phytoplankton abundance where salinities above ~ 2 g/L induced shifts from *Daphnia* to rotifer dominance in Danish brackish lagoons. These results are opposite to the trend we observed in the Alberta lakes, yet Evans *et al.* (1996) found large-bodied zooplankton in Redberry Lake, a deep saline (20 g/L) lake in Saskatchewan, thrived due to limited competition from other zooplankton at high salinity and they grazed phytoplankton biomass to below predicted levels. There is evidence of light limitation in some of the study lakes (Moquin and Jackson, unpublished data) yet Brushy Lake was very turbid (135 NTU) and extremely productive ($\text{Chl}_a = 246 \mu\text{g/L}$), indicating that light limitation does not apply to all study lakes.

Turbidity

The weak relationship between nephelometric turbidity and chlorophyll *a*, yet strong correlation with TSS, clearly shows that turbidity was not dominated by phytoplankton (Table 4.2, Fig. 4.3). Turbidity increased with TDS while the organic

content of TSS declined from fresh to saline lakes (TDS 0-10 g/L) indicating that the increase in TSS was due to suspended mineral content rather than zooplankton or organic detritus. Sediment resuspension was likely common in the more saline lakes since macrophytes appeared to be sparse, if present, (personal observation) to anchor sediments and impede water movement (Scheffer, 1998). Turbid, saline wetlands dominated by suspended sediments, rather than phytoplankton, have also been observed in Australia (Strehlow *et al.*, 2005). Lower organic content in lakes with higher turbidity and salt concentrations is consistent with the known effects of osmotic stress on freshwater organisms as salinity concentrations increase to 10 g/L (Hammer *et al.*, 1983; Williams *et al.*, 1990; Hart *et al.*, 1991) and to reduced biodiversity and productivity of individual species (Fernandes, 1993). However, at the community level, osmotic stress would not have necessarily reduced organic content in saline lakes since a few salt tolerant species could have become be very productive as a result of lower competition with salt sensitive species (e.g. Evans *et al.*, 1996). High phytoplankton biomass in Brushy Lake (TDS = 41.3 g/L) indicates that osmotic stress cannot be the sole driver of reduced biomass at high salinities in the study lakes.

The strong correlation between turbidity and TSS suggests that much of the lakes' TP results from sediment resuspension and internal loading (Wetzel, 2001). High pH in the lakes could also promote P-loading by reducing Fe-P binding at the sediment-water interface (Lijklema, 1977). Sulphate concentrations were high in many of the lakes and can be associated with phosphorus release from the sediments and increased concentrations in overlying water (Caraco *et al.* 1989). Sulphate concentrations in the six shallow lakes with low TDS were relatively low (0.06 - 0.6 g/L) compared to much

higher concentrations (0.4 - 17.3 g/L) in lakes where TDS > 2.5 g/L and TP was very high.

TN was not correlated with turbidity and only weakly correlated with TSS, but it was strongly correlated with TDS. In estuaries, higher salinities have been associated with increased ammonium release from the sediments, possibly due to ion pairing between salt ions and ammonium that helps neutralize the ammonium ion and facilitates diffusion into the water column (Gardner *et al.*, 1991). Here, similar processes may also promote ammonia diffusion from the lake sediments. The association between nitrogen and salinity could also arise from agricultural run-off that becomes concentrated within the water column due to high evaporation. In saline Redberry Lake, Saskatchewan, large-bodied zooplankton (*Diaptomus sicili* and *Daphnia pulicaria*) dominated zooplankton populations (Evans *et al.*, 1996). While their intense grazing depressed phytoplankton populations and the N pool within the phytoplankton community, the zooplankton biomass in the lake was up to 7.9 times higher than predicted based on nutrient and chlorophyll models. Because of high N:P stoichiometry for the two dominant zooplankton species (>26; Sterner and Elser, 2002), they represented a potentially important nitrogen reservoir.

Heterocystous cyanobacteria

Phytoplankton biomass was highest (Chl *a* > 50 µg/L) in four shallow lakes with low sulphate concentrations. Phytoplankton biomass was frequently low in lakes with high TDS, but high TDS was also associated with high sulphate concentrations, with the exception of Brushy Lake, which was unique among the high salinity lakes because it had

low sulphate concentrations and exceptionally high phytoplankton concentrations, including a high abundance of heterocystous cyanobacteria.

The absence of heterocystous cyanobacteria in many of the 20 shallow lakes may have resulted from high sulphate concentrations. Molybdenum-dependent nitrogenase is responsible for most biological nitrogen fixation (Igarashi and Seedfelt 2003) but sulphate can competitively inhibit uptake of stereochemically similar molybdenum by uptake enzymes (Marino *et al.*, 2003). Evans and Prepas (1997) argued that $\text{SO}_4^{2-} : \text{MoO}_4^{2-}$ ratios in saline lakes of central Alberta were not sufficiently high to reduce MoO_4^{2-} uptake rates during nitrogen fixation but rather high pH and alkalinity caused low iron bioavailability which, in turn limited nitrogenase synthesis and nitrogen fixation. However, this mechanism appears inconsistent with our results from Brushy Lake where pH and alkalinity were exceptionally high yet heterocystous cyanobacteria supported the highest phytoplankton biomass. Recent research by Marino *et al.* (2003) proposed that high sulphate concentrations, rather than sulphate: molybdenum ratios, inhibit molybdenum uptake rates as molybdate assimilation was inhibited at sulphate concentrations $> 8 \text{ mM}$ ($\sim 768 \text{ mg/L}$). Only seven of the 20 shallow lakes studied here had sulphate concentrations $< 768 \text{ mg/L}$. The four lakes containing high proportions of heterocystous cyanobacteria had sulphate concentrations ranging from 380-620 mg/L. The remaining three lakes with low sulphate concentrations may not have contained high proportions of heterocystous cyanobacteria for a number of other reasons such as phosphorus limitation or high zooplankton grazing (Marino *et al.*, 2006). It is possible that phytoplankton biomass in the 12 shallow lakes with sulphate concentrations $> 768 \text{ mg/L}$ was also limited by low nitrogen bioavailability or problems with nitrogen

assimilation but they were not able to fix nitrogen due to high (1350 - 17 270 mg/L) sulphate concentrations leading to inhibited molybdate assimilation.

A regional model

TP-phytoplankton relationships can vary among lakes due to factors other than phosphorus that affect phytoplankton growth (e.g. light, other nutrients, temperature, zooplankton grazing and salinity). Evans *et al.* (1996) proposed the development of regional predictive models that account for regional variations in drivers of phytoplankton biomass. Robarts *et al.* (1992) also call for new TP – chlorophyll *a* models in western saline lakes. Bierhuizen and Prepas (1985) proposed a nutrient-chlorophyll model for saline lakes in Alberta, but their model does not apply to lakes with low N:P ratios, as seen in this study. Here, I propose modifications (Fig. 4.9) to the alternate regimes conceptual model developed for lakes in northern Europe (Scheffer *et al.*, 1993), which address differences in drivers of phytoplankton biomass and turbidity in saline shallow lakes of southern Alberta compared to lakes of northern Europe. In particular, I focus on salinity, alkalinity and pH, resuspended sediments, phytoplankton, turbidity and benthic algae. The compartments of the Scheffer *et al.* model (1993) that I did not address deserve attention in future work.

Prairie lakes vary greatly in salinity and, in southern Alberta, ion composition likely impacts phytoplankton biomass in shallow lakes. High sulphate concentrations appear to impair nitrogen availability and nitrogen fixation while high magnesium concentrations may reduce phosphorus availability. High total salt concentrations likely create osmotic stress, which could reduce phytoplankton biomass in some species if

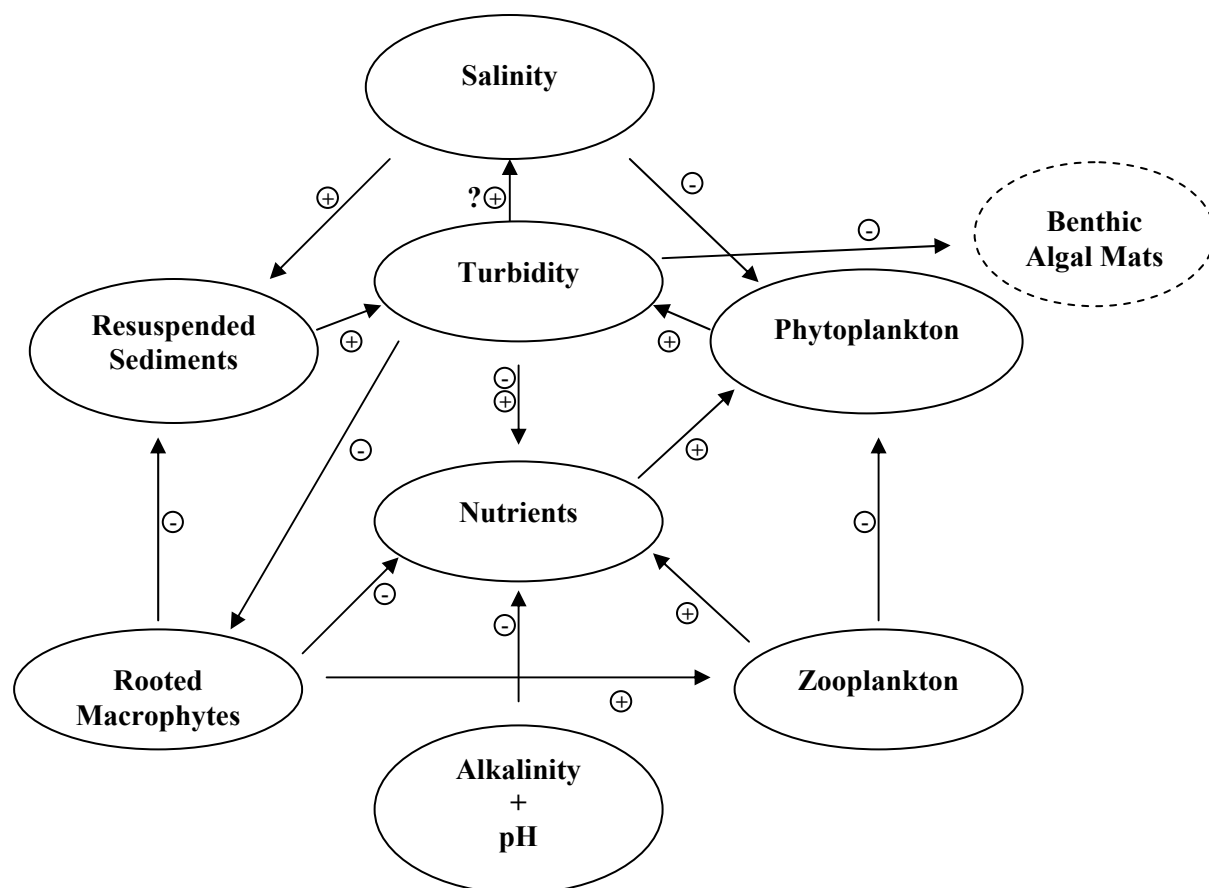


Figure 4.9. A conceptual model of factors affecting turbidity in southern Alberta's shallow saline lakes. This model modifies the conceptual model proposed by Scheffer *et al.* (1993). By adding salinity, alkalinity + pH, and benthic algal mats and modifying rooted macrophytes and phytoplankton. Here, increases in salinity reduce phytoplankton biomass but appear to increase turbidity through non-phytoplankton sources. Abundant alkalinity and high pH may have negative impacts on nutrient availability and, as a consequence, phytoplankton biomass and its contribution to turbidity. Increased turbidity likely has negative impacts on benthic algal mats. Rooted macrophytes are explicitly identified to distinguish them from non-rooted, floating vegetation and phytoplankton are specified to distinguish them from benthic and periphytic algae.

energy is diverted to osmoregulation (Fernandes, 1993). Salinity can also reduce biodiversity and alter species composition among phytoplankton, macrophytes zooplankton and macroinvertebrate communities (Hammer *et al.*, 1983; Williams *et al.*, 1990; Hart *et al.*, 1991). Though not measured here, trace metals such as bioavailable iron and molybdenum would be useful parameters to measure in future research as they are key components of nitrogen assimilation and fixation enzymes (Igarashi and Seedfelt, 2003). I did not consider seasonal fluctuations in salinity, but the salinity of some shallow lakes in southern Alberta does increase over the summer (personal observation). Lakes with wide fluctuations in salt concentration would favour phytoplankton and zooplankton species with wide salinity tolerances and would likely have lower levels of biodiversity compared to lakes with relatively stable salt concentrations (Aladin, 1991; Floder and Burns, 2004). A model designed to estimate phytoplankton-dominated turbidity in shallow lakes of southern Alberta should consider these salinity-related impacts on phytoplankton abundance.

In conclusion, a number of shallow saline lakes in southern Alberta do not exhibit the alternate macrophyte-dominated clear and phytoplankton-dominated turbid regimes that are seen in shallow lakes of northern Europe. First, turbidity in the shallow saline lakes that I studied in southern Alberta was not always dominated by phytoplankton. This violates one of the key assumptions of the 1993 model (Scheffer and van Nes, 2007). My research suggests that, if lakes do maintain regimes, at least a third regime where turbidity is dominated by inorganic seston likely exists. Second, phytoplankton abundance in the southern Alberta lakes was not strongly linked to concentrations of nutrients commonly considered in the alternate regime models (TN, TP) when salinity

was greater than $\sim 2.5\text{g/L}$. This was likely because the chemistry in these saline lakes either renders nutrients biologically unavailable and/or prevents phytoplankton from assimilating them. In chapter three I concluded that there is no convincing evidence that the lakes studied existed in alternate clear and turbid regimes in 2007 or that they shifted between turbid and clear regimes over the past 150 years. This chapter presented some possible mechanisms that may explain why the saline shallow lakes in southern Alberta do not exist in alternate regimes. If multiple regimes do exist in shallow lakes of southern Alberta, they are most likely governed by water chemistry (ion composition and concentrations as well as trace metals, pH and alkalinity) more so than by nutrients alone.

CHAPTER FIVE: CONCLUSION

My research has shown limited evidence for regime shifts in the shallow lakes that I studied, it helps clarify the role of internal and external processes on water quality in shallow prairie lakes and it provides field support for recent research into sulphate impacts on nitrogen-fixation in cyanobacteria. This study also questions the utility of TN and TP measurements in the study lakes and points toward opportunities to investigate the relationship between purple sulphur bacteria and phytoplankton abundance in shallow prairie systems.

Major Findings

I found limited evidence of regime shifts in the study lakes. In chapter three I asked whether the changes in water quality over time were consistent with the theory of alternate stable regimes in shallow lakes. Five lakes showed the possibility of a dramatic shift from clear to turbid conditions. “Space for time” analyses did not provide any evidence of a bimodal distribution of lakes between clear and turbid regimes. One reason for these results is that phytoplankton does not dominate turbidity in many of the study lakes.

External forces likely drove increases in productivity and turbidity observed in most study lakes since 1850 while either internal or local processes likely governed more acute, asynchronous changes in water clarity. Nine of the 10 lakes examined clearly became more eutrophic between 1850 and today (chapter two). However, the onset of eutrophication differed across lakes as did the magnitude of the changes. Results from

water quality sampling across 20 lakes showed that even among those lakes that demonstrated eutrophication, some lakes are presently oligotrophic (clear) while others are hypereutrophic (turbid). These differences indicate that local or internal processes moderated the regional drivers of increased turbidity and productivity. One explanation may be that agriculture has been a regional driver of change since the late 1800s but was introduced in the catchments of individual lakes at different points in time over that period. This explanation is not strongly supported when I compare the timing of the most dramatic water quality changes in adjacent lakes (e.g. Hilton Long and Hilton West; Appendix B). An alternate explanation is that differences in internal lake structure and processes made individual lakes more or less susceptible to external drivers. For example, chapter four highlighted the role of internal chemistry through the potential inhibition of nitrogen fixation when sulphate concentrations are high. Differences across lakes are likely due to a combination of both local external and internal factors.

Heterocystous cyanobacteria were only abundant in lakes with low sulphate concentrations (< 8 mM). These field results support laboratory findings that high sulphate concentrations inhibit molybdenum uptake rates and was limiting to nitrogenase enzymes as molybdate assimilation was inhibited at sulphate concentrations > 8 mM (Marino *et al.*, 2003). My results differ from a previous field study that suggested that nitrogen fixation in saline waters of Alberta is inhibited by high pH and alkalinity that causes low iron bioavailability (Evans and Prepas, 1997) as I found heterocystous cyanobacteria abundant in some lakes with very high pH and alkalinities. Future research on this topic should include analysis of iron and molybdenum concentrations.

Total nutrient (TN, TP) measures were not informative in this study. Nutrients often limit lake productivity and TN and TP are often used to predict productivity and, to some extent, community composition. In this study, total nutrient concentrations were extremely high, but biologically available nutrients appeared to be low in many lakes. Therefore, nutrient-based alternate regime models were not applicable to these lakes and future work with models should include analysis of biologically available nutrients in addition to total values. Nutrients may have been limiting in some of the study lakes due to low biological availability, but it is also possible that phytoplankton biomass was limited by other factors, such as light.

Sulphur plays an important role in the ecology of the study lakes. High sulphate concentrations appear to inhibit nitrogen fixation (chapter four). This may be due to competitive inhibition of molybdenum uptake by nitrogenase but, especially given high pH found in the study lakes, it also could result from low bioavailable iron if most iron has precipitated as FeS. However, okenone data from sediment cores (chapter two) indicates growth of purple sulphur bacteria populations over time, suggesting that they likely play an increasingly important role in sulphur cycling in these study lakes. Some purple sulphur bacteria can oxidize H_2S and FeS when it is abundant. Depending on the purple sulphur bacteria present in the study lakes, it is possible that they prevent iron precipitation. Iron is implicated in nitrogen fixation, nitrate assimilation and other biological processes, and also reduces phosphate mobilization from sediments. There are other considerations too; for example, sulphur reducing bacteria may also be present in the study lakes and would benefit the purple sulphur bacteria by converting sulphate to

sulphides. There is much unknown about the microbial loop and related nutrient cycles in the study lakes and there's much opportunity for research within them.

Future Research

It will be important to identify what factors limit phytoplankton biomass accumulation in these lakes. I expected that nutrients limited phytoplankton biomass accumulation in the study lakes but that may not be the case. Additional research is needed to determine whether phytoplankton biomass is limited by biologically available nutrients, light, zooplankton grazing or other factors such as micronutrients. My research points to potential mechanisms that could explain limitation by nutrient bioavailability, but I did not investigate the mechanisms themselves and such research could be valuable. I would also further investigate the potential role of sulphate inhibition of nitrogen fixation in these lakes. A better understanding of what limits phytoplankton biomass accumulation in these lakes would improve success and reduce costs of eutrophication management.

I did not study benthic microbes explicitly yet as I analysed my data it became increasingly clear that benthic microbes likely play a key role in the ecology of the lakes. In future research I would characterize the benthic microbial communities and investigate their roles in biogeochemical cycles in these lakes.

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APPENDICES

Appendix A. Asynchronous Onset of Eutrophication Across Shallow, Prairie Lakes of Southern Alberta

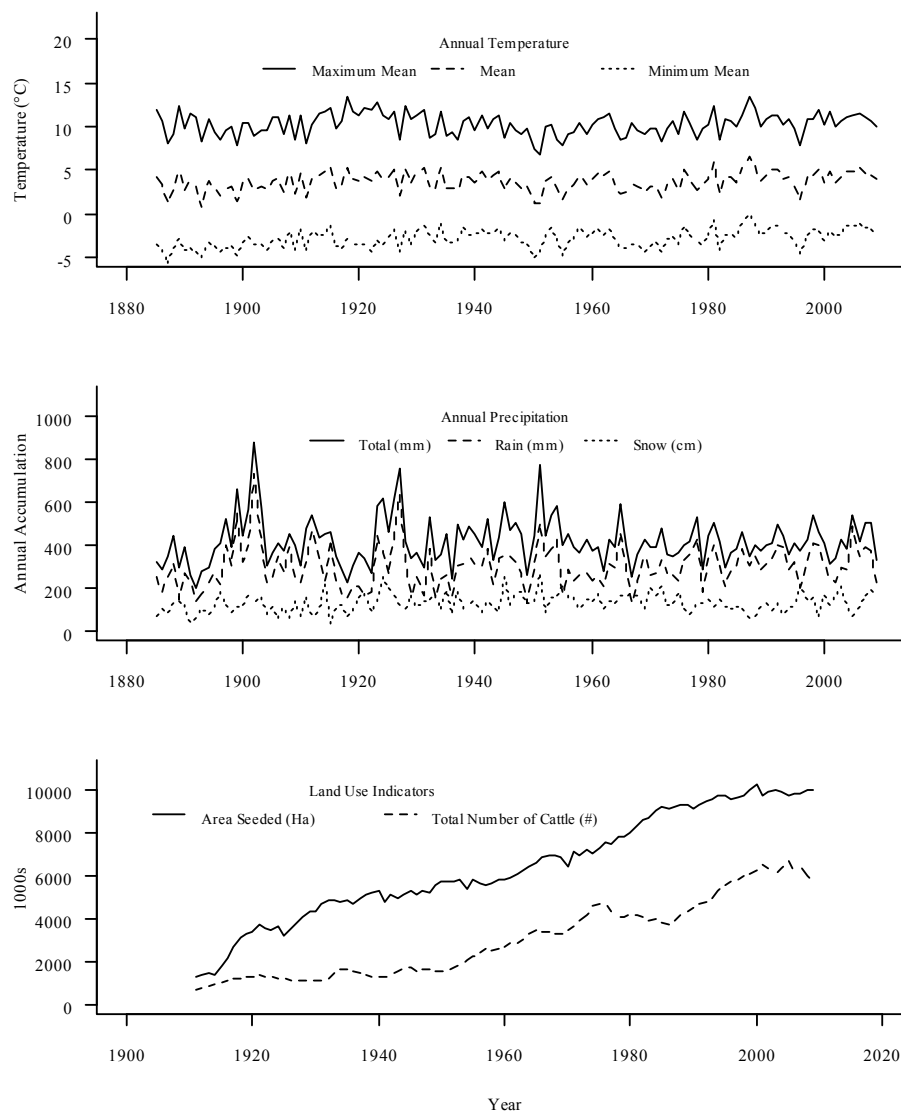


Figure A.1. Historical weather and land use trends. Panel a. Trends in annual temperature in southern Alberta (Calgary International Airport). Maximum mean = annual mean of maximum daily temperatures, mean temp = annual mean of daily mean temperatures, and min mean = annual mean of minimum daily temperatures. Source: Environment Canada. Panel b. Trends in annual precipitation in southern Alberta (Calgary International Airport). Total = total annual precipitation, Rain = total annual rainfall, Snow = total annual snowfall. Source: Environment Canada. Panel c. Long-term data for the area of land seeded in Alberta (thousands of hectares) and the number of cattle reported on Alberta farms (thousands). Source: Statistics Canada

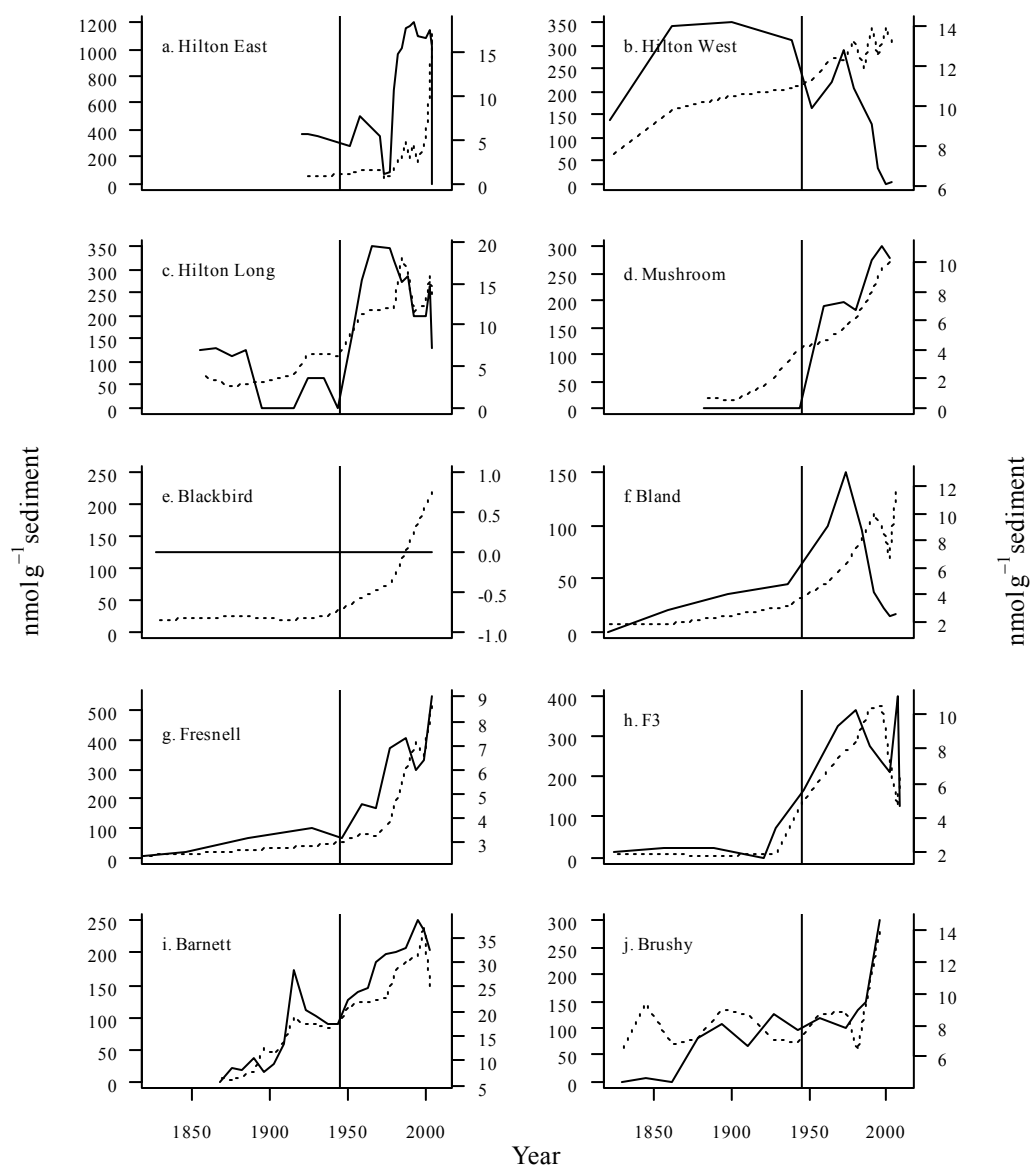
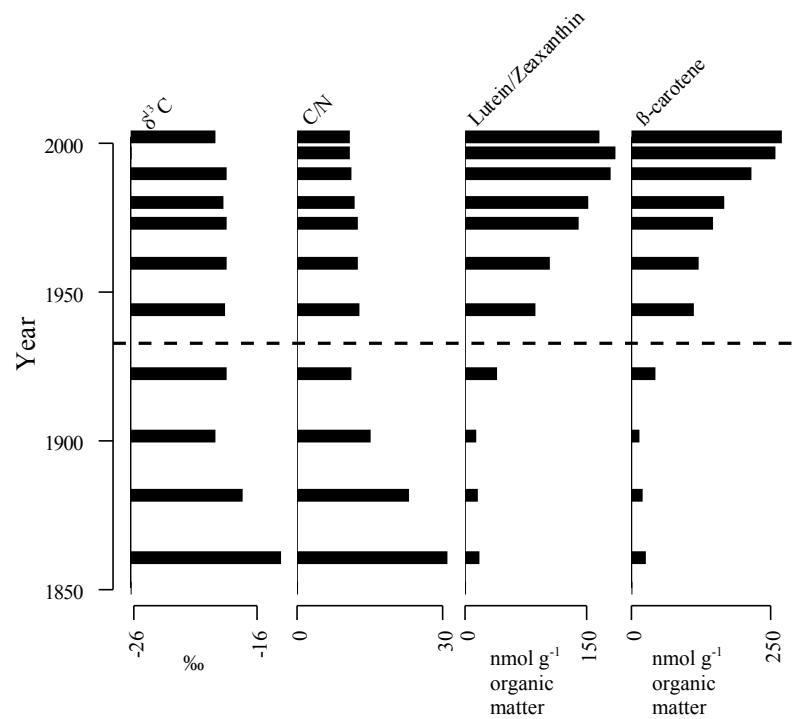


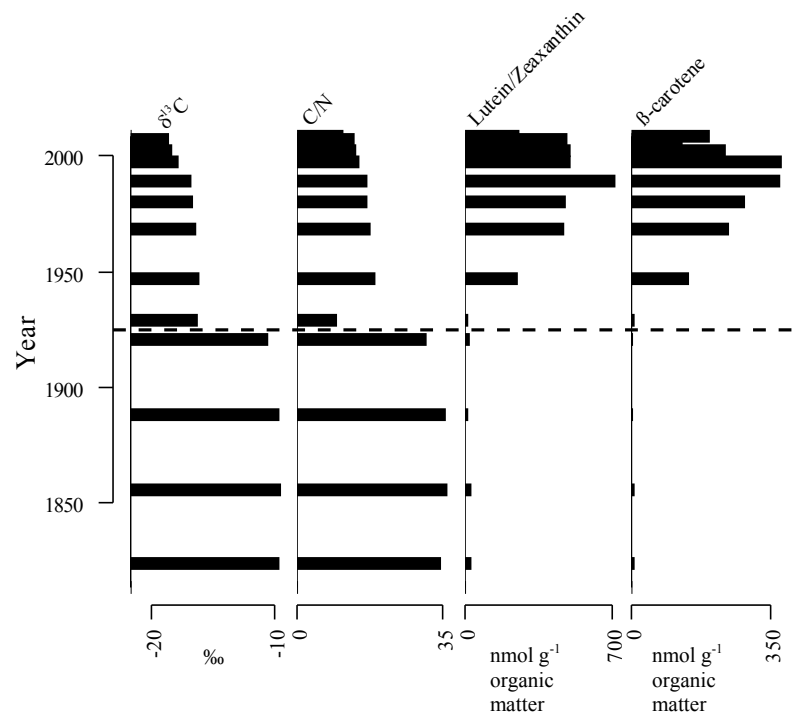
Figure A.2. Trends in plant and algal biomass (β-carotene concentrations; dotted lines) and purple sulphur bacteria biomass (okenone; solid lines) in the study lakes between 1850 – 2008 based on fossil pigment analyses. Horizontal lines mark the onset of the GA (1945).

Appendix B. Limited Evidence of Alternate Regimes in Alberta’s Shallow, Southern Prairie Lakes

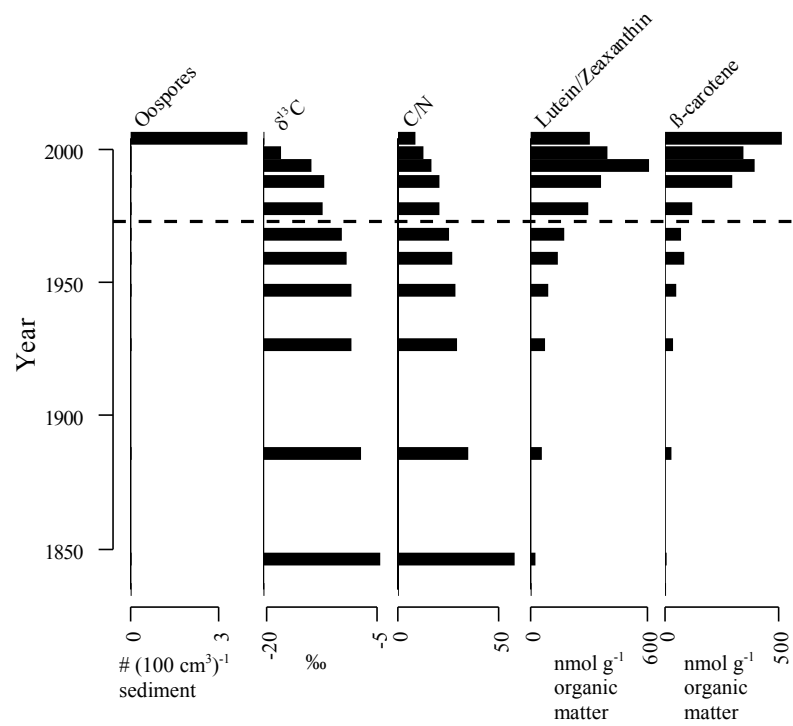
a. Mushroom



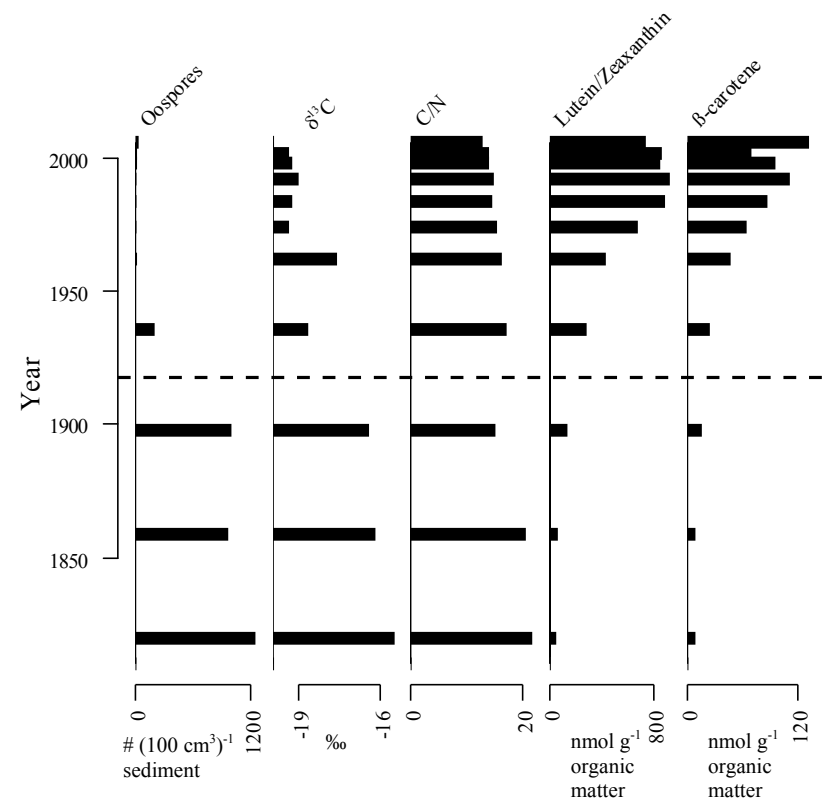
b. F3



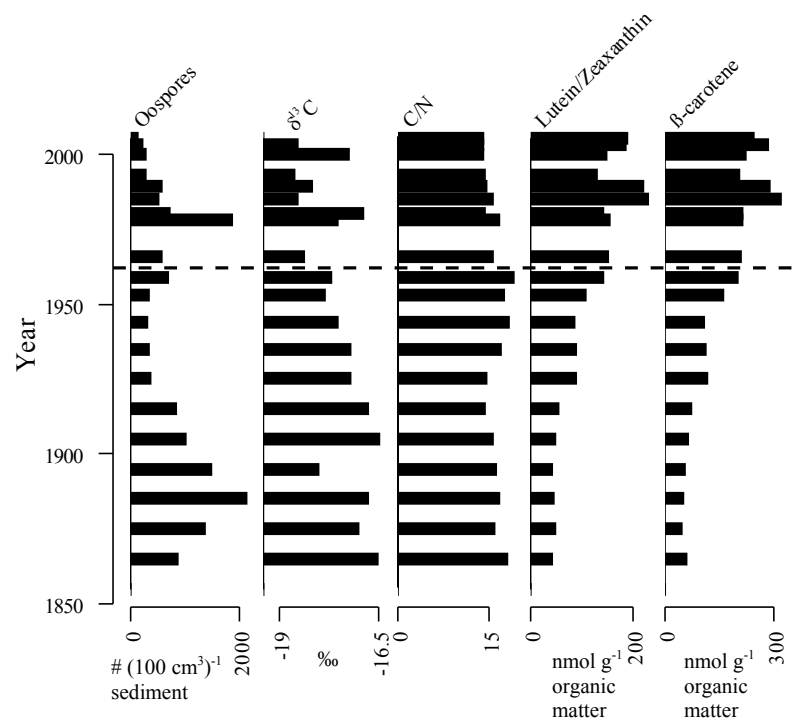
c.Fresnell



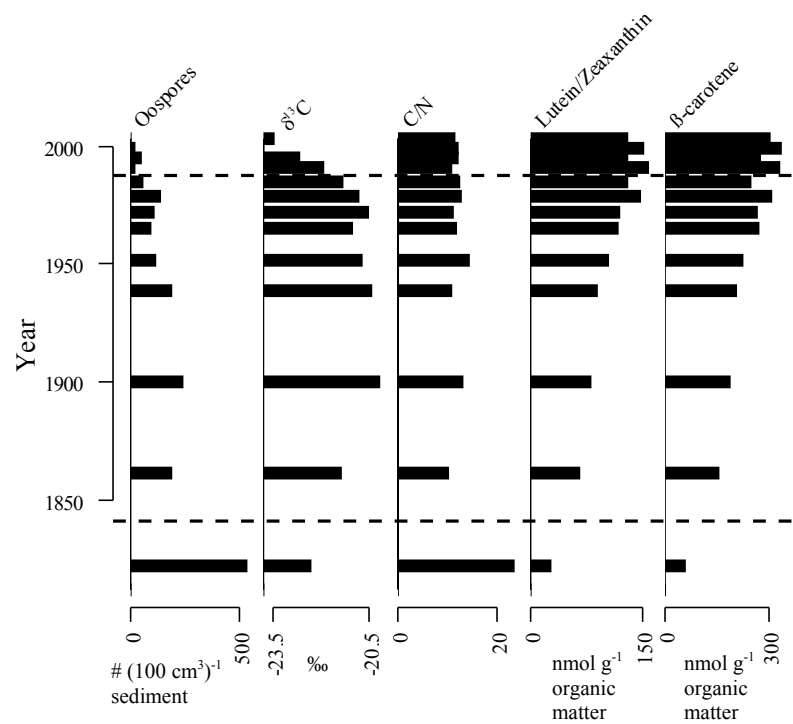
d. Bland



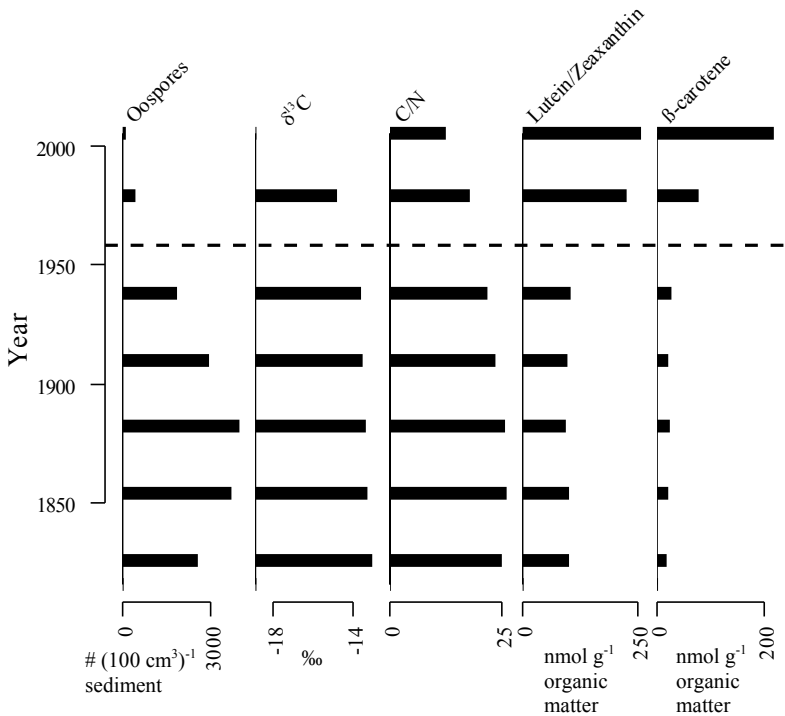
e. Hilton Long



f. Hilton West



g. Blackbird



h. Brushy

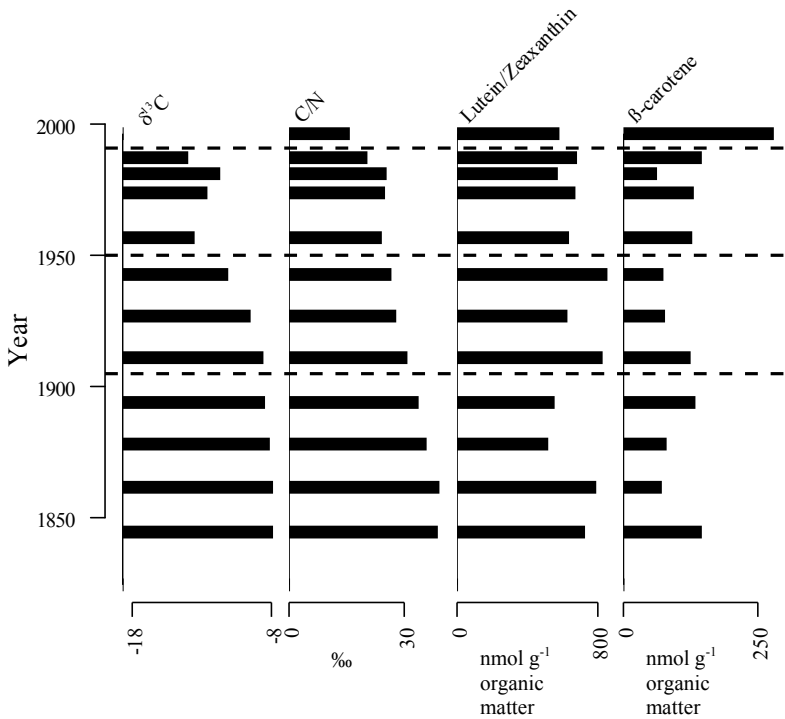


Figure B.1. Sediment proxies used as indicators of change in phytoplankton and macrophyte abundance over the past 150 years in 8 lakes from southern Alberta. Graphs reflect changes in proxy abundance over time. Lines crossing all proxies indicate cluster breaks and may represent shifts between water clarity regimes. Oospores (#/100 cm³ sediment), Delta 13 C ($\delta^{13}\text{C}$ ‰), C/N (Carbon:Nitrogen ratio), Lutein/Zeaxanthin (nmol g⁻¹ organic matter), β -carotene (nmol g⁻¹ organic matter).

Appendix C. Salinity Effects On Turbidity and Implications for Alternate Regime Models

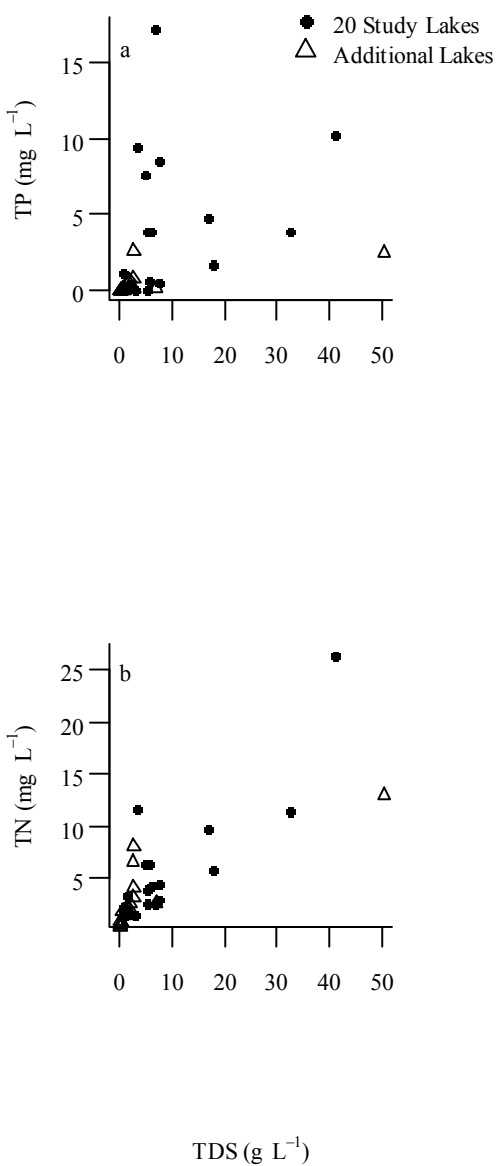


Figure C.1. Relationships between TDS and TP (a) and TDS and TN (b) across 20 shallow lakes in southern Alberta sampled in August, 2007 (black circles) and 17 deep and shallow lakes sampled by Alberta Environment over a broader geographic area (open triangles).

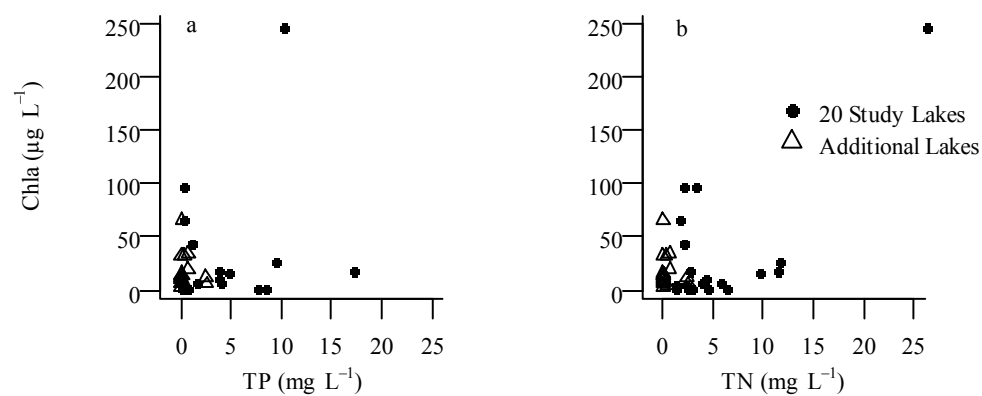


Figure C.2. Relationships between TP and chlorophyll *a* (a) and TN and chlorophyll *a* (b) across 20 shallow lakes in southern Alberta sampled in August, 2007 (black circles) and 17 deep and shallow lakes sampled by Alberta Environment over a broader geographic area (open triangles).

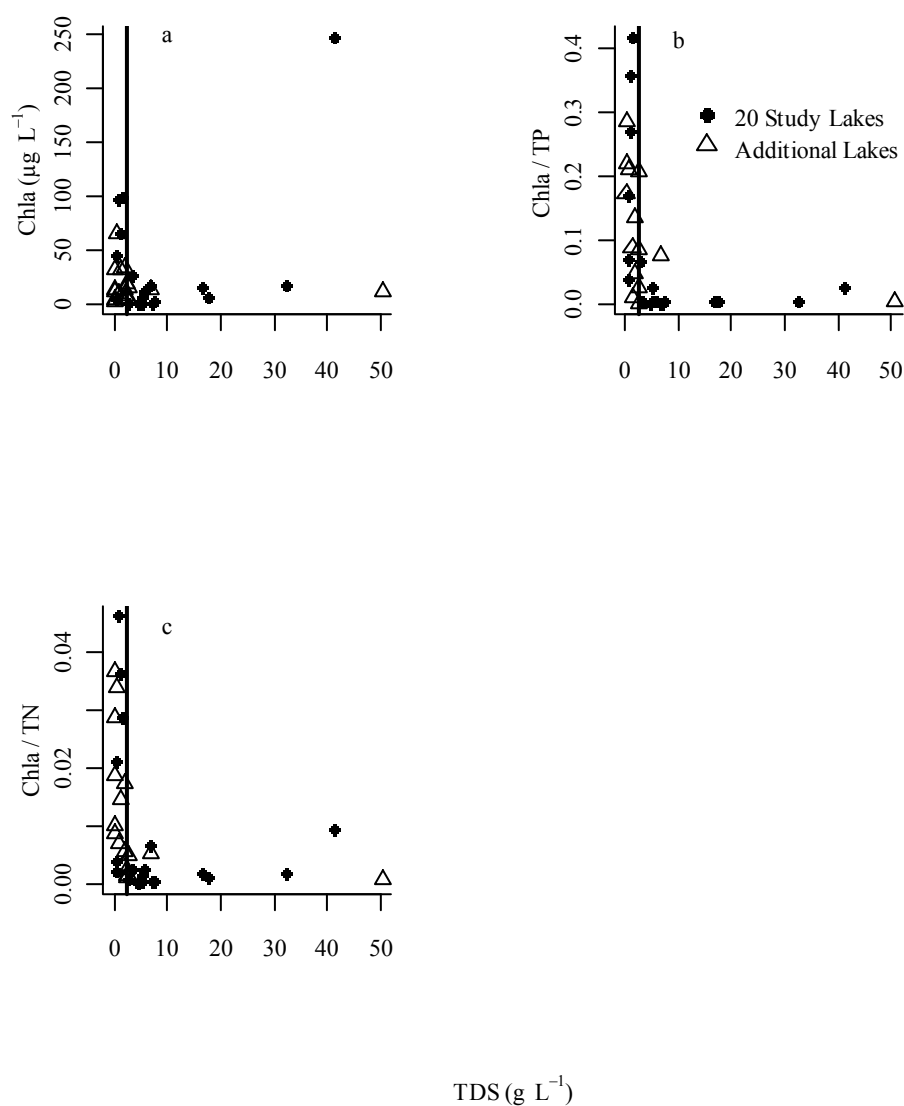


Figure C.3. Relationships between TDS and chlorophyll *a* (a), TDS and chlorophyll *a* /TP (b), TDS and chlorophyll *a* /TN (c) and TDS and chlorophyll *a* /SRP (d). Water samples were taken from the 20 shallow lakes in southern Alberta in August, 2007 (black circles) and 17 deep and shallow lakes sampled by Alberta Environment over a broader geographic area (open triangles). Bars indicate TDS = 2.5 g /L and represent the concentration at which salinity has been hypothesized to impair nitrogen fixation (Evans and Prepas, 1996).