University of Alberta

Factors driving switches in the primary producer communities of shallow lakes of the Boreal Plains, Alberta, Canada

by

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Abstract

The mechanisms that contribute to the frequent switching of primary producer communities in shallow lakes on the Boreal Plains of Alberta, Canada were explored. The lakes tend to be clear and macrophyte-rich (61% of lakes) or turbid and phytoplankton-rich (30% of lakes). The study is based on surveys of twenty-three lakes on the Boreal Plains, Alberta, Canada monitored from 2001 to 2007.

I examined the effect of annual fluctuations in precipitation on the limnological conditions of the study lakes and the primary producer communities. Drought concentrated nutrients, phytoplankton biomass and turbidity, decreasing macrophytes cover and promoting a phytoplankton-rich regime. Macrophyte abundance was better predicted by lake depth. During the study SAV cover increased with lake depth and was significantly higher in 2007 following three years of high water levels. Precipitation-induced switches occur because the lakes are small, isolated and the water budget is dominated by precipitation inputs and evaporative outputs with little surface or groundwater fluxes.

The lake and landscape factors affecting the persistence of the macrophyte-rich regime and phytoplankton-rich regime were assessed. The macrophyte-rich regime was more persistent in shallow lakes (max. depth < 112 cm) with high macroinvertebrate predator biomass (> 580 μg L^{-1}) and low TP concentration (< 58 μg L^{-1}) (variance explained = 0.66). Lakes with high *Daphnia* dominance (> 61% of the Cladocera community) and higher TP concentration (> 67 μg L^{-1}) were associated with a more persistent phytoplankton-rich regime (variance explained = 0.50).

I examined the importance of food web structure in maintaining the alternative regimes. Food web structure appears important in maintaining the resilience of the macrophyte-rich regime in fishless lakes on the Boreal Plains. The macrophyte-rich regime is reinforced (stabilized) by top-down control of phytoplankton and periphyton by macroinvertebrates and zooplankton. In contrast, food web effects appear weak or absent in the phytoplankton-rich regime.

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Chapter 1 – **Introduction**

Alternative stable state theory

Understanding the response of an ecosystem to environmental changes is one of the major goals of ecosystem management. All ecosystems are exposed to gradual changes in environmental conditions such as climate, inputs of nutrients or toxic chemicals, reduction of groundwater inputs, habitat fragmentation, harvest or loss of species diversity. The state of an ecosystem may respond in a linear way to changing environmental conditions (Figure 1-1a), or in a non-linear way (Figure 1-1b). If an ecosystem has more than one stable community composition in the same external environmental conditions, it is said to have alternative stable states (ASS), with an unstable equilibrium between the states (Figure 1-1c) (Scheffer et al. 2003).

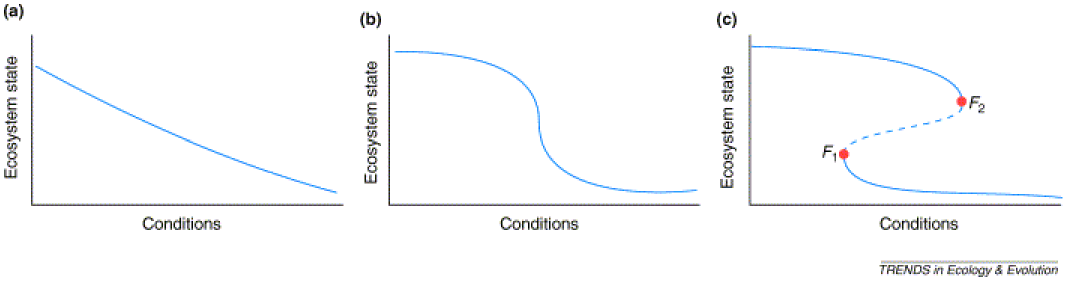

Figure 1-1. Different ways that an ecosystem can respond to a change in environmental conditions (Scheffer et al. 2003). A system may shift between alternative stable states at the bifurcation point (F_2) and induce a catastrophic shift to the lower alternative state ('forward shift'). If one tries to restore the state on the upper branch by means of reducing the conditions the system shows hysteresis. A backward shift only occurs if conditions are reversed far enough to reach the other bifurcation point, F_1.

The concept of ASS emerged from work on theoretical models (Lewontin 1969; Holling 1973; May 1977). However, proof for the existence of ASS in natural ecosystems is difficult to demonstrate as it requires the interfacing of phenomena that occur on different scales of time, space and ecological organization (Levin 1992; Scheffer et al. 2001). An observation of a large shift is not sufficient because such systems may also be responding in a non-linear, threshold manner (Figure 1-1b). Additional evidence for ASS may include observations of repeated shifts, studies of positive feedback mechanisms maintaining the states, models showing that mechanisms can plausibly explain field data, or rigorous experimental tests (Scheffer et al. 2001). The term 'regime shifts', originally proposed in oceanic systems to describe sharp changes to changing conditions around some critical threshold (Steele 1996; Hare et al. 2000), is increasingly used in the general sense to refer to sudden drastic transitions from one ecosystem regime to another. Several studies have provided a strong case for alternative regimes in various ecosystems including shallow lakes (Scheffer et al. 1993), forests and savannas (Staver et al. 2011), coral reefs (Hughes 1994; Bellwood et al. 2004) and kelp forests (Simenstad et al. 1978).

Ecosystems that exhibit regime shifts may be sensitive to disturbances if the conditions are close to the regime boundaries. Often these shifts are catastrophic with little warning, and almost always identified in retrospect. However, recent research has revealed early changes may occur that may serve as ecological indicators before the regime shift is complete (Carpenter et al. 2011; Carpenter et al. 2011; Seekell et al. 2011). Once a switch has occurred, the ecosystem may exhibit hysteresis. Hysteresis is where the environmental conditions need to be brought back further, beyond the switch point, to return a system to its' original state (Scheffer et al. 2001; Scheffer et al. 2003). A system that might be easily pushed into a different state from which it may be more difficult to restore is clearly challenging from a management perspective (Beisner et al. 2003).

The regime of an ecosystem or community can be characterized by any number of community variables based on *a priori* knowledge and what one wishes to learn about the system (Beisner et al. 2003). The amount of community change is specified based on what can be detected statistically and is considered ecologically meaningful. Regime variables can be defined in a number of ways including temporally or spatially averaged abundances of species or guilds (e.g. average chl-*a* concentration in August), spatial coverages (e.g. percent cover of submerged aquatic vegetation in August) or organic or inorganic variables (e.g. turbidity values). Where alternative regimes occur, the selected set of variables will persist in one of a number of different possible configurations, or in other words, at different equilibrium points that are locally stable (Beisner et al. 2003).

Mechanisms for regime switches

Alternative regime switches may occur in two ways (Scheffer et al. 2001; Beisner et al. 2003). The first way is if a sufficiently large perturbation is applied directly to the community variables (Figure 1-1, vertical axis), wiping out parts of populations. An example in shallow lakes is shifts that have occurred when winterkill events in Minnesota, USA have eradicated fathead minnow populations leading to a clear water state. The same lakes reverted to a turbid state dominated with phytoplankton with subsequent fish colonization events (Zimmer et al. 2001). Abundant fish populations or other top predators can have strong effects on the entire food web, causing profound shifts in species abundance on various trophic levels. Thus frequent regime switches may be related to the interplay between the effects of top predator and changes in lake conditions. The second way ecosystem state switches may occur is when perturbations cause fluctuations in the control variables (Figure 1-1, horizontal axis) that determine the behaviour of regime variables and the ways they interact with each other. This situation occurs if there are changes to environmental "drivers" that influence the communities. Additional effects may be a change in the number and location of alternative regimes that may occur. An example in shallow lakes is water level fluctuations in two shallow lakes in southern Sweden that coincided with alternative regime switches (Blindow 1992). Increased water levels decreased light availability for SAV (regime variable) leading to a switch to a turbid regime dominated by phytoplankton. Declines in the water level improved the light conditions for SAV and the lakes reverted to a clear water regime (Blindow 1992).

The likelihood of a perturbation resulting in a shift to an alternative regime depends on the size of the perturbation and the resilience of the regime. 'Resilience' can be defined as the collective attributes of a system including (1) the amount of change that a system can absorb while still maintaining the same structure and function, (2) the system's ability to self-organize, and (3) the degree to which a system is capable of adaptation (Holling 1973; Scheffer et al. 2001). Lewontin (1969) conceptualized the resilience of a system using a ball-in-a-cup portrait. A rolling ball represents the trajectory of a community that rolls towards the stable state, represented by the lowest point on the landscape. Resilience is positively related to the steepness and depth of the basin. Loss of resilience is depicted by shallowing and flattening of the basin (Beisner et al. 2003). Gradual environmental changes like eutrophication or climate change may reduce the resilience of a system and make it more vulnerable to a regime shift.

Alternative regimes in shallow lakes

Shallow lakes are widely regarded as a classic example of ecosystems exhibiting alternative regimes (Scheffer et al. 1993; Carpenter et al. 1999; Chase 2003). One regime is dominated by submersed aquatic vegetation (SAV) with clear water at low total phosphorus (TP) concentrations, and the other regime is dominated by phytoplankton with high turbidity at high TP concentrations, but at intermediate phosphorus concentrations either state may exist (Figure 1-2). High increases in total phosphorus, most often from human-induced eutrophication, has been associated with a sudden loss of transparency and SAV and dramatic shifts to a phytoplankton-dominated regime (Scheffer et al. 1993; Jeppesen et al. 1999). Loss of animal diversity and high algal biomass makes this regime undesirable (Scheffer et al. 2001).

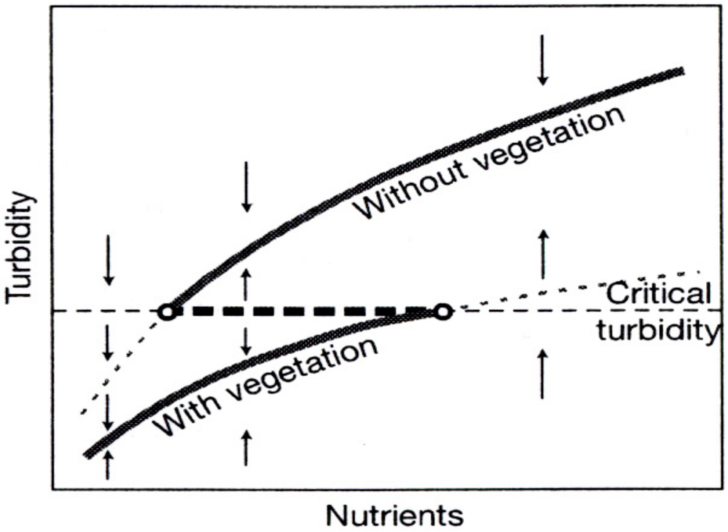

Figure 1-2. Alternative equilibrium related to the presence and absence of vegetation.

Competitive interactions between SAV and phytoplankton for light and nutrients are thought to be the core mechanisms maintaining the alternative regimes in shallow lakes (Scheffer et al. 1993). Phytoplankton biomass decreases light penetration, limiting SAV growth below a (turbidity dependent) depth and limiting lake coverage (Phillips et al. 1978; Eminson et al. 1980; Jeppesen et al. 1990; Scheffer et al. 1993). Because shallow lakes are often ubiquitously shallow the exceedance of a turbidity threshold often results in the switching of state of an entire lake.

A suite of self-stabilizing mechanisms between SAV, phytoplankton and their environment help stabilize the alternative regimes and provide internal resistance to regime shifts (Figure 1-3) (reviewed by (Scheffer et al. 1993). SAV provides structure to the lake that clearly differentiates the clear and turbid water regimes (Moss 1990). Macrophytes help maintain the clear water regime through a number of mechanisms including promoting piscivore control of planktivorous fish (Andersson et al. 1978; Blindow 1992), providing a predation refuge for zooplankton that graze on phytoplankton (Burks et al. 2002), and reducing sediment resuspension (Barko et al. 1998). Perennial vegetative structures enable growth the following year further maintaining the state from year-to-year (Jeppesen et al. 1997). In contrast, when the same lakes have high concentrations of nutrients, phytoplankton blooms appear to competitively exclude macrophytes through rapid nutrient uptake and re-release of phosphorus leading to algal blooms and shading (Jeppesen et al. 1997; Scheffer 1998). In turbid lakes, planktivorous fish are central in maintaining the regime. They promote phytoplankton growth through the consumption of zooplankton and the rapid recycling of nutrients. Fish, especially benthic fish, such as carp, and waves also stir up sediments when there is no vegetation present. Light limitation caused by algae blooms and disturbance of the sediments make it difficult for vegetation to establish (Jeppesen et al. 1997; Jeppesen et al. 1998; Scheffer 1998; Moss 2010).

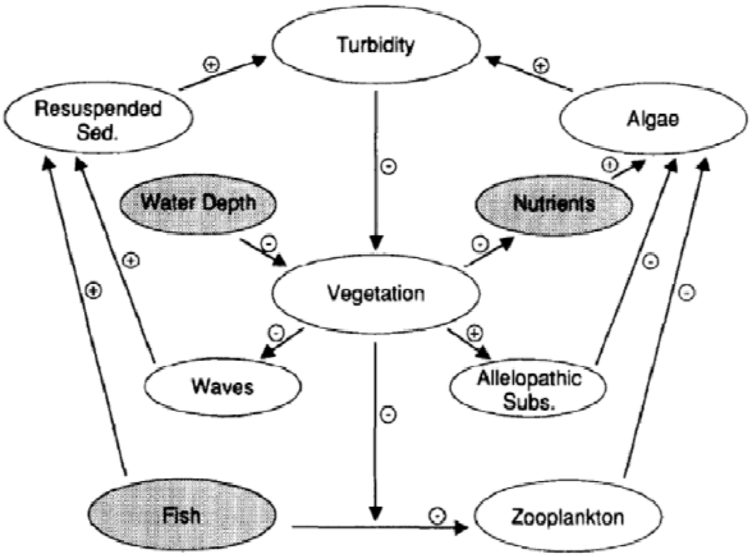

Figure 1-3. Positive feedback loops thought to maintain the existence of alternative stable states in shallow lakes (Scheffer et al. 1993).

Shallow lakes on the Boreal Plains

Shallow lakes and wetlands on the Boreal Plains of Canada cover up to 50% of the landscape (National Wetlands Working Group 1988). These aquatic ecosystems are important features of the landscape, regulating flows, removing nutrients and silt, and providing important wildlife habitat (Kalff 2002; Mitsch et al. 2002). They provide one of the most important waterbird habitats in North America (Ducks Unlimited Canada 2011).

Human development is expanding in the Boreal Plains due to recent advances in the forestry, and oil and gas industries. These industries will impact shallow lakes through activities such as timber harvesting, road construction, seismic exploration, and construction of well sites, pipelines and other infrastructure (Schneider 2002). Additionally, climate warming has increased over the past century and near future warming is predicted to impact water quantity and quality in the region (Schindler et al. 2006). Anthropogenic activities may alter the flux of water, sediment and nutrients to shallow lakes, which may affect their community composition and functioning (Schindler 2001).

Shallow lakes in the Boreal Plains show evidence of the existence of alternative regimes (Bayley et al. 2003; Bayley et al. 2007). The alternative regimes follow a nutrient gradient, such that clear, SAV-rich lakes tend to occur at low TP concentrations whereas turbid conditions with high phytoplankton biomass tend to occur in eutrophic to hypereutrophic lakes. A synoptic survey identified two additional alternative regimes – a high phytoplankton and high

SAV regime, and a low phytoplankton and low SAV regime (Bayley et al. 2003). Alternative regimes in shallow lakes are typically persistent over time (Andersson et al. 1978; Blindow 1992; Scheffer et al. 1993; Hargeby et al. 2007). However, Bayley *et al.* (2007) found that the majority of lakes in the Boreal Plains have highly transient alternative regimes, with 7% switching once and 73% switching 2-9 times over a 20-year period. Inter-annual switches in phytoplankton biomass were related to total phosphorus (TP), but were also dependent on the abundance of SAV (Bayley et al. 2003; Bayley et al. 2007).

Overview of research questions and approach

Shallow lakes are complex systems. Lake attributes, such as area, nutrient status, and hydrologic contributions from precipitation and groundwater sources, vary across the landscape. Lake conditions are affected by internal processes and dynamics, such as nutrient cycling, competition for light and nutrient, and predator effects on lower trophic levels. Added to the spatial heterogeneity, are the chaotic dynamics of fluctuating climatic conditions. Understanding the interplay of internal lake processes, external landscape factors, and the extrinsic forces of climate, all of which may be operating on different timescales, is clearly challenging.

I was interested in understanding the mechanisms that contribute to alternative regime switches in Boreal Plains lakes. The high frequency of switches in a predominantly pristine environment suggests that small perturbations in climate may be important in driving the switches. Furthermore, the internal positive feedback mechanisms that maintain the ecosystem states in shallow lakes of temperate North American and Europe may be weak (i.e. the states lack resilience).

I identified my research questions and hypotheses based a literature review of shifting mechanisms in other shallow lake systems and my understanding of the local study system. Below, I provide an overview of my rationale, key research questions, study approach, and hypotheses.

Chapter 2 – Effects of a top invertebrate predator on fishless pond ecosystems

The majority of shallow lakes in the Boreal Plains are fishless due to the harsh winter conditions that result in fish kills (Conlon 2002; Tonn et al. 2004). Large predatory macroinvertebrates are top predators in shallow fishless lakes where they are abundant and diverse compared to fish-bearing water bodies (Mallory et al. 1994; Batzer et al. 1996; Mittelbach et al. 2004). The macroinvertebrate community was largely ignored in the initial model of Scheffer et al. (1993). However, studies indicate that predatory macroinvertebrates are a critical factor affecting the species composition of prey communities in shallow fishless waterbodies (Wellborn et al. 1996). Studies have found macroinvertebrate predators capable of causing top-down effects via consumption of zooplankton to phytoplankton (Arner et al. 1998), and via macroinvertebrate grazers to periphyton (Blaustein et al. 1995; Stav et al. 2000). Additionally, evidence suggests that macroinvertebrate grazers may have an important role in suppressing epiphyton and maintaining high macrophyte biomass in clear water lakes (Jones et al. 2003). Few studies have examined the role of macroinvertebrate predators and grazers in maintaining alternative regimes in fishless shallow lakes.

Chapter 2 investigates the role of *Dytiscus alaskanus*, a top macroinvertebrate predator in fishless lakes of the Boreal Plains, in helping to maintain the alternative regimes. I investigated the top-down effects of *D. alaskanus,* on the abundance, community composition and diversity of lower trophic levels. Experiments were performed in mesocosms in six fishless shallow lakes. The densities of *D. alaskanus* were manipulated and the effects on macroinvertebrates, zooplankton and phytoplankton and periphyton populations were monitored over six weeks. I also performed laboratory experiments to determine *D. alaskanus* feeding preferences when presented with a variety of prey options.

I predicted that *D. alaskanus* would be a generalist predator and consume a wide variety of invertebrate taxa in the field experiment leading to decreased macroinvertebrate biomass. Snails are common in the study ponds and the consumption of snails by *D. alaskanus* was predicted to lead to an increase in periphyton biomass, similar to trophic cascades observed in other benthic communities (Brönmark 1994; Nystrom et al. 2001; Jones et al. 2003). I predicted that dytiscids would consume other macroinvertebrate predators due to their higher trophic position (Hornung 2008). Whether these top-down effects would cascade down to zooplankton and phytoplankton was unknown.

Chapter 3 - Lake and landscape factors affecting the persistence of alternative regimes

I was interested in how lake and landscape factors affected the persistence of alternative regimes. Switches between alternative regimes are often induced by an external forcing factor, such as eutrophication or a change in lake level, but the persistence of each regime may be reinforced (stabilized) by internal positive feedback mechanisms (Moss 1990; Scheffer et al. 1993). The rapid and repeated regime shifts observed in shallow lakes on the Boreal Plains (Bayley et al. 2007) suggests that internal mechanisms providing internal resistance to external changes in other shallow lakes are weak or lacking. Top-down effects mediated by fish play a central role in maintaining alternative regimes in the initial model of Scheffer et al. (1993). However, the majority of shallow lakes in the Boreal Plains are fishless due to the harsh winter conditions which result in fish kills (Conlon 2002; Tonn et al. 2004). Few studies have examined the importance of food web structure in maintaining alternative regimes in fishless shallow lakes. I hypothesized that the SAV-rich regime would be associated with fishless lakes with a rich macroinvertebrate community that suppresses epiphyton. In contrast, the phytoplankton-rich regime would be associated with fish-bearing lakes with reduced zooplankton grazers and increased phytoplankton biomass, consistent with Scheffer et al. (1993) original conceptual model of positive feedback mechanisms maintainting alternative states in shallow lakes.

I was interested in how spatial variability in lake features would affect the persistence of alternative regimes to regional changes in climate (the primary disturbance affecting the study region) over time. A lake district is a landscape rich in lakes that share a common origin, climate, and catchment geology. Yet despite these common features, lakes within a district vary considerably in their physical, chemical and biological characteristics. Lake features ranging from internal features such as food web structure and nutrient cycling to morphometry and the interaction between a lake and its catchment may be the causes of spatial variability within a district.

Lakes on the Boreal Plains are sensitive to fluctuations in inter-annual precipitation due to constraints imposed by the climate and landscape. The relatively flat topography, glacially derived sediments, and sub-humid climate produce low runoff (Redding and Devito 2008). The lakes are small, shallow, and isolated. The hydrologic budgets of a moraine lake and lowland organic lake were dominated by precipitation inputs (83 – 95%) and evaporative outputs (93 – 96%). Lateral groundwater exchange between the surrounding peatlands and the lakes constituting the remainder of the water fluxes, with negligible surface water runoff (< 1%) (Ferone et al. 2004). Evaporative concentration of nutrients and organic matter in isolated lakes is an important mechanism influencing phytoplankton production, as seen in other boreal lakes (Schindler et al. 1996), in Lake Vortsjarv, a large shallow lake in Estonia (Noges et al. 1999) and several floodplain lakes (Sokal et al. 2008; Loverde-Oliveira et al. 2009; McGowan et al. 2011). Shallow groundwater inputs from adjacent peatlands can be important source of water and phosphorus to shallow lakes on the Boreal Plains (Ferone et al. 2004). Drought conditions are attenuated in lakes connected to large peatlands due to shallow groundwater flow reversals (Ferone et al. 2004).

I hypothesized that the persistence of alternative regimes to inter-annual changes in precipitation would depend on a lake's relative sensitivity to drought. The SAV-rich regime would be more persistent in lakes that were resistant to drought, whereas the phytoplankton-rich regime would be more persistent in lakes that were more sensitive to drought. Lake sensitivity to drought was predicting to increase with decreasing lake size and maximum depth (Wolfe et al. 2007), increasing elevation in the landscape (Webster et al. 2000), decreasing groundwater connectivity (Kratz et al. 1997), and decreasing shallow ground water connection with adjacent peatlands (Ferone et al. 2004). Finally, the heterogeneity of surficial geology types (glaciofluvial > morainal > organic) may affect a lake's sensitivity to drought through the integration of landscape features such as lake position, extent of wetlands in the buffer, and/ or lake morphometry.

The study is based on a survey of twenty-three lakes on the Boreal Plains, Alberta, Canada monitored from 2001 to 2007. The first objective was to determine the internal feedback mechanisms that are helping to stabilize alternative regimes in shallow lakes on the Boreal Plains. The lakes were classified as SAV-rich or SAV poor, and phytoplankton-rich or phytoplankton poor using previously established thresholds. This study expands on the work of Bayley and Prather (2003) and Bayley *et al.* (2007) by examining the biotic communities in more detail over a longer time. We focused on food web mechanisms that help maintain alternative regimes in shallow lakes of earlier studies to identify potential causes for the frequent switches observed in shallow lakes on the Boreal Plains.

The second objective was to determine the lake and landscape features that best predict the persistence of the alternative regimes in shallow lakes on the Boreal Plains. Regime persistence was the percentage of time that each lake was dominated by SAV and phytoplankton from 2001 to 2007. We tested key lake-variables identified from the first objective (maximum lake depth, standard deviation of lake depth, TP, dominance of *Daphnia* within the Cladocera community, macroinvertebrate predator biomass, and fish prevalence) and key landscape variables (lake elevation, surface water connectivity, groundwater connectivity, wetland extent and dominant surficial geology type in local catchment, and lake area) to determine the best predictors of alternative regime persistence using regression tree analysis. Understanding whether landscape attributes can be relied on to predict lake conditions and dynamics is a priority for addressing environmental issues at regional scales (Vitousek 1994).

Chapter 4 – Precipitation induced alternative regime switches

Recent studies have focused on unravelling the mechanisms behind natural regime shifts in shallow lakes. Climate induced changes in water levels has been identified as a natural trigger for regime switches. Water level decreases generally increases water clarity resulting in increased SAV coverage (Blindow 1992; Blindow et al. 1993; Van Geest et al. 2003; Van Geest et al. 2007), whereas water level increases tends to reduce light availability leading to decreased SAV coverage (Wallsten et al. 1989; Engel et al. 1994).

The high frequency of switches in a relatively pristine environment suggests that small perturbations in climate drive the switches on the Boreal Plains. A synoptic survey suggested a water depth effect on the dominance of primary producers – the shallowest lakes supported high phytoplankton and high SAV, lakes with moderate water levels were either clear with high SAV or turbid with low SAV depending on the TP levels, and the deepest lakes had low SAV and phytoplankton (Bayley et al. 2003). The climate and landscape setting of shallow lakes in the Boreal Plains may make them sensitive to fluctuations in precipitation. The lakes are small and predominantly isolated, and the water budget is dominated by precipitation inputs (83 – 95%) and evaporative outputs (93 – 96%) based on hydrologic research on two shallow lakes in the study area (Ferone et al. 2004). Inter-annual differences in precipitation are likely to affect the concentration of nutrients and other limnological variables in these lakes. Lake water is nutrient-rich reflecting shallow groundwater inputs from adjacent wetlands and peatlands (Ferone et al. 2004), whereas precipitation is nutrient poor (Ferone 2001). Wetter conditions were correlated with lower phytoplankton biomass in lakes on the Boreal Plains (Sass et al. 2008) suggesting a dilution effect.

This study aimed to identify how shallow lakes in the Boreal Plains respond to inter-annual fluctuations in precipitation, the key abiotic and biotic drivers of phytoplankton biomass and SAV abundance, and a mechanism for the frequent lake regime switches. This chapter is based on a survey of 23 lakes sampled annual from 2001 to 2007. I explore the effect of fluctuations in annual precipitation on the regional lake response including water depth, nutrient concentration, turbidity, phytoplankton biomass, SAV abundance, and the percent of phytoplankton and macrophyte dominated lakes on the landscape. Secondly, I investigate the effect of key lake conditions on phytoplankton biomass and SAV abundance to better understand the lake conditions driving the switches between the alternative regimes. Finally, I propose a mechanism for the frequent lake regime switches in shallow lakes on the Boreal Plains based on the responses of the lake conditions to inter-annual changes in climate, and the key drivers of phytoplankton biomass and SAV abundance. I studied many lakes over several years, creating a powerful approach that allowed me to assess shallow lake dynamics at a landscape scale.

I hypothesized that years with low annual precipitation would lower lake levels, concentrating TP and leading to increased phytoplankton biomass (chl-*a*), higher turbidity, and decreased SAV cover. Wet years should increase lake levels, diluting TP, decreasing chl-*a* and turbidity, and favouring SAV growth.

Chapter 5 – General discussion and conclusions

In the final chapter I review the major findings of my research studies. I explore how this study contributes to the field of shallow lake ecology. Shallow lake ecosystems have served as an important ecological system to illustrate stability dynamics that may be relevant to other ecosystems that are not be so easily studied, such as coral reefs (Scheffer et al. 2001; Folke et al. 2004).

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Chapter 2 - **Effects of a top invertebrate predator (*Dytiscus alaskanus*; Coleoptera: Dytiscidae) on fishless pond ecosystems**[1]

Introduction

Top predators can have substantial effects on species lower down in the food web (Power 1990; Persson 1999), either through direct predation or indirect effects. Some prey species can be reduced through direct consumption by predators, thus resulting in positive effects on primary producers, while other consumers increase in abundance through competitive release (Paine 1966; Paine 1969). Trophic cascades occur when a change in the top predator shifts predation pressures to alternate links in the food chain, so increased predator pressure on herbivores leads to an increase in plant biomass (Power 1990; Carpenter et al. 1998).

Studies of the freshwater habitat gradient indicate that predatory invertebrates are a critical factor affecting the species composition of prey communities in shallow fishless waterbodies (Wellborn et al. 1996). Large predatory macroinvertebrates, including dytiscid beetles (Dytiscidae), dragonfly larvae (Odonata), and true bugs (Hemiptera), are top predators in these aquatic systems and are abundant and diverse compared to fish-bearing water bodies (Mallory et al. 1994; Batzer et al. 1996; Mittelbach 1998; Kalff 2002).

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[1] A version of this chapter has been published at www.springer.com. Cobbaert, D., S.E. Bayley and J.-L. Greter. 2010. Hydrobiologia 644(1): 103-114.

Studies have found invertebrate predators capable of causing a trophic cascade. *Notonecta* was observed to cause a trophic cascade via *Daphnia* to phytoplankton (Arnér et al. 1998) and via mosquito larvae to periphyton (Blaustein et al. 1995). Stav et al. (2000) observed a dragonfly larvae – mosquito larvae – periphyton cascade. However, Vanni and Findlay (1990) found that *Chaoborus* consumed *Daphnia* but these top-down effects did not cascade down the food chain to phytoplankton. Shurin (2000) also found that *Notonecta* predator effects on zooplankton did not extend to phytoplankton. This study further investigates the impact of large invertebrate species on the abundance, species composition and diversity of prey communities and their indirect food web effects in these fishless systems.

Adult *Dytiscus* sp. are top invertebrate predators in boreal fishless ponds in the study region. They occupy the highest trophic position in the food web based on stable isotope analyses (Hornung 2008) and have the highest biomass of all predaceous invertebrates (Hornung et al. 2006). *Dytiscus alaskanus* dominates dytiscid communities (Aiken 1991) and occurs in a wide variety of aquatic habitats across Alberta (Larson 1985). *D. alaskanus* has several characteristics that make them well suited as top predators in boreal ponds including their large size (22.6 – 30.2 mm), a short lifespan as larvae when they are most vulnerable to predators, a hard cuticle and defensive secretions, which make them resistant to predators (Larson et al. 1990). Insect predators, including dytiscid beetles, tend to be generalists that will prey on nearly all other invertebrates, including each other

(Batzer et al. 1996). The prey preferences of adult *D. alaskanus* have not previously been studied.

Our overall objective was to determine the predatory effects of a large invertebrate species on the abundance, species composition and diversity of pond communities, and to assess whether those effects were strong enough to propagate to different trophic levels. The first goal of the study was to determine the direct effects of *D. alaskanus* predation on invertebrate biomass and community composition. We tested this effect in two ways. First we performed a field experiment where we manipulated *D. alaskanus* densities and examined the effects on invertebrate prey. Secondly, we performed laboratory experiments to determine *D. alaskanus* feeding preferences when presented with a variety of prey options. Our second goal was to test the indirect effects of *D. alaskanus* on the abundance of lower trophic levels including zooplankton and primary producers (phytoplankton and periphyton) in the field experiment, and ultimately to evaluate the potential of *D. alaskanus* to maintain top-down control of various trophic levels in fishless ponds and therefore to propagate a trophic cascade.

We predicted that *D. alaskanus* would be a generalist predator and consume a wide variety of invertebrate taxa in the field experiment leading to decreased macroinvertebrate biomass. Snails are common in the study ponds and the direct consumption of snails by *D. alaskanus* was predicted to indirectly increase periphyton biomass, similar to trophic cascades observed in other benthic communities (Bronmark 1994; Nystrom et al. 2001; Jones et al. 2003). We predicted that dytiscids would consume other macroinvertebrate predators due to their higher trophic position (Hornung 2008). Whether these top-down effects would cascade down to zooplankton and phytoplankton was unknown.

Methods

Study area

The study area is in north-central Alberta, Canada (56º52"N, 115º27"W), a predominately pristine area in the boreal forest with little human disturbance. The ponds were randomly selected from a suite of twenty-three small fishless ponds that had been previously studied (Norlin et al. 2005). The six study ponds are small (1.3-7.0 ha, average = 5.7 ha) and shallow (centre depth = 136 ± 59 cm; mean ± standard deviation). The trophic conditions are mesotrophic to eutrophic - total phosphorus concentrations average 45.8 ± 17.7 µg L-1, chlorophyll *a* concentrations average 5.1 ± 4.6 µg L-1, and total nitrogen concentrations are high (1637 ± 338 µg L-1) (mean ± standard deviation based on samples collected from the six ponds on four occasions). The total nitrogen to total phosphorus ratios average 18 ± 8, suggesting phosphorus limitation. An average pH level varies from 6.2 to 8.7. The ponds are warm with moderate oxygen levels just below the surface (7.8 mg ± 1.9 L^{-1}) and an average Secchi depth of 85 ± 26 cm.

Field experiment

The predator effects of *Dytiscus alaskanus* on the community composition and biomass of phytoplankton, periphyton, zooplankton and macroinvertebrates were investigated using mesocosms in six ponds. Two replicate predator treatments and two control treatments were nested within each of the six ponds for a total of 24 mesocosms. The predator treatment consisted of equal quantities of male and female adult *D. alaskanus* added at a density of 1 beetle/ 25 L to 800L mesocosms. This density was within the range of natural densities based on quantitative surveys of aquatic habitats in the region (D. Cobbaert, unpubl. data; (Aiken et al. 1985). The control treatment lacked adult *D. alaskanus.*

Mesocosms (1-m^3) were constructed out of clear polyethylene curtains and suspended from wooden frames with floats that were placed along an 80cm depth contour in each pond. The bottom was covered with 2-mm mesh netting to exclude benthic predators while allowing nutrients to seep into the mesocosm. The mesh on the bottom of the mesocosms permitted natural densities of small phytoplankton and zooplankton access to the mesocosms during installation. Macroinvertebrates (excluding Dytiscidae adults and larvae) were collected from several locations within each pond to a density consistent to the mesocosms, pooled in one container, mixed, and then added randomly to each mesocosm. One sample from the pooled container was retained to characterize the initial macroinvertebrate communities. *Ceratophyllum demersum* (350-g wet weight) was added to each mesocosm to provide habitat for the macroinvertebrates. A piece of wood (60-cm x 6-cm) was added to each mesocosm to provide a perch for the dytiscid beetles. Two-mm light mesh netting covered the top of the mesocosms to prevent the dispersal of flying invertebrates, particularly *D. alaskanus*. The enclosures likely inhibited predator and prey interactions (internal community dynamics), and dispersal movements (metapopulation dynamics). Habitat selection preferences (including immigration and emigration) are a critical process determining biodiversity and community structure of aquatic beetles

(Binckley and Resetarits 2005), thus the experimental results may differ from natural ponds. Efforts were made to approximate pond conditions – they were large (800-L), similar depths (80-cm) and predator and prey densities approximated natural pond densities. The experiment ran over a six-week period from June 26, 2005 – August 12, 2005, which coincided with peak phenology of *D. alaskanus* in the study region (Aiken 1991).

The mesocosms and ponds were sampled for water chemistry every two weeks. Water samples were chilled and processed within 8 hours of collection. Water chemistry analyses were conducted at the Biogeochemical Laboratory at the University of Alberta following standardized procedures (Stainton et al. 1977; Bergmann et al. 1980; Prepas et al. 1982) for the following variables: chlorophyll a, phosphorus (total phosphorus (TP), total dissolved phosphorus (TDP), and soluble reactive phosphorus (SRP)), and nitrogen (total nitrogen (TN), total dissolved nitrogen (TDN), nitrite and nitrate, and ammonium). Chlorophyll *a* concentration was used as an estimate of phytoplankton biomass. Chlorophyll was extracted in 95% ethanol and analyzed with a spectrophotometer at 750, 665, and 649 nm. Temperature, pH, dissolved oxygen, and electrical conductivity were measured in the field using a Hydrolab Quanta field probe (Hydrolab Corporation, Austin, Texas, U.S.A.).

Zooplankton was sampled from each mesocosm on the first day of the experiment and subsequently every two weeks. Zooplankton samples (2-L) were collected with an acrylic tube (135 x 6.5 cm^2) (Swanson 1978), passed through 64-µm mesh netting, and preserved with a 4% formalin-sugar solution (Prepas

1978). Sub-samples were collected with a wide-bore trigger pipette and enumerated with a counting wheel. Zooplankton was identified with a Wild M5 (40X magnification) dissecting scope (Wild Heerbrugg, Switzerland). Zooplankton was identified to genera with Thorp & Covich (2001); Cladoceras and copepods were identified to species (Edmondson 1959). Zooplankton was categorized into four length classes (0.63 - 0.9 mm, 0.9 - 1.45 m, 1.45 - 2.05 mm and more than 2.05 mm). Numbers were converted to biomass using the length-weight regressions of McCauley (1984).

Macroinvertebrates were sampled on the first day of the experiment from a pooled sample and subsequently every two weeks from each mesocosm. Macroinvertebrates were sampled with two upward vertical sweeps with a standard D-shaped invertebrate dip net (640 cm^2 opening, 500-µm mesh size). Samples were chilled on ice and were sorted from vegetation within 8 hours of sampling and preserved in 70% ethanol. Macroinvertebrates were counted and identified to genera or species, except for Diptera, which were identified to family (Clifford 1991; Merritt et al. 1996; Thorp et al. 2001). All macroinvertebrate specimens were measured for wet weight and converted to dry weights using a reference collection of at least 30 individuals that were dried at 60° C and weighed to the nearest 0.0001g.

Periphyton was collected from each mesocosm on the last day of the experiment. The mescocosms were gently raised above the water surface and periphyton was scraped with a scalpel from 3 quadrats (100 cm^2) on the south aspect of the mesocosm walls approximately 10 cm below the water surface. The subsamples were pooled and quantified using reversed-phase high-performance liquid chromatography (HPLC) using standard techniques (Leavitt et al. 1994).

Statistical analyses

Mesocosm effects were tested by comparing values of limnological variables (temperature, electrical conductivity, pH, dissolved oxygen, secchi depth, water depth, total nitrogen, total phosphorus, and dissolved organic carbon) between mesocosms and their associated ponds. Limnological values from four sampling periods were averaged for each site and compared with a multivariate analysis of variance (MANOVA). When significant multivariate effects were found then univariate ANOVA and Tukey post-hoc tests were used to determine treatment differences.

Phytoplankton biomass, periphyton biomass (only week 6), zooplankton biomass and species richness, total macroinvertebrate biomass and species richness, and predator macroinvertebrate biomass were subjected to linear mixed effects modelling (R Development Core Team 2007). Linear mixed effects models tested for treatments effects (fixed factor) nested within ponds (random factor) over time (repeated effects, random factor) for each of the response variables (Pinheiro et al. 2004). Linear mixed effects models are useful in cases where there is temporal pseudoreplication (repeated measures) as they allow for temporal autocorrelation across repeated measures on the same subjects (in this case mesocosms).

Data were log transformed if necessary to improve normality. A Bonferroni correction was applied to adjust for the total number of response variables tested.

Feeding preference laboratory experiments

Laboratory experiments were used to determine adult *Dytiscus alaskanus* feeding preferences of invertebrate prey communities from different ponds. These experiments were used to determine whether the predator effects observed in the mesocosm experiment were a direct result of Dytiscid feeding preferences. If beetles could be shown to have a preference for certain invertebrate prey species then a decrease in these prey species within the dytiscid treatment mesocosms would likely be the direct result of predation and not due to other indirect biological interactions. Prey communities vary amongst ponds and the feeding preferences of predators vary depending on which prey are offered. Patterns in the size and mobility of the preferred prey taxa from different pond communities would form a generalized picture of dytiscid feeding preferences.

Invertebrate communities from three of the mesocosm study ponds were presented to the dytiscids in four different experiments. We sampled the invertebrate communities from the ponds from August 29 – September 1, 2005 using a standard D-net along random areas of the shoreline. The macroinvertebrates were identified and enumerated, and the most common invertebrate taxa from each pond formed the prey community for the laboratory experiments.

Each experiment was tested for two fixed factors - prey taxa and predator sex. Within an experiment each aquarium received a prey community, which consisted of 5 individuals of all dominant prey taxa. One dytiscid beetle was added to each aquarium; males and females were tested in equal quantities and randomly assigned. Each aquarium represented a replicate within each experiment. The first experiment had 8 replicates (4 males; 4 females) and a prey community that included: Corixidae (*Sigara* sp.), *Daphnia*, Ephemeroptera (*Caenis* sp.), Gastropoda (*Physa* sp.), and Zygoptera (*Coenagrion* sp.). The second experiment had 10 replicates (5 males; 5 females) with a prey community of Ephemeroptera (*Caenis* sp.), *Gammarus lacustris* G.O. Sars, Gastropoda (*Physa* sp.), *Hyallela azteca* Saussure, Hydrachnidia, and Trichoptera (*Triaenodes* sp.). The third experiment had 6 replicates (3 males; 3 females) with a prey community of Corixidae (*Sigara* sp.), *Chaoborus* sp., and *Daphnia* sp. A fourth experiment had 9 replicates (5 males; 4 females) and compared two different amphipod species – the smaller *Hyallela azteca* and the larger *Gammarus lacustris;* ten individuals of each prey species were offered in this experiment. Different individuals of prey species and dytiscids were used in all replicates and experiments.

The feeding preferences were determined using cafeteria experiments (Krebs 1998). Five-liter aquariums were filled with 4 L of off-gassed tap water; aerators were added to ensure adequate oxygen levels, and two plastic plants with 4 stems each were added to provide refugia for prey and perches for the dytiscids. Dytiscids were starved for 48 hours to standardize their level of hunger and then added to the aquariums. The number of prey remaining within each aquarium was observed and recorded at 1, 6, 12 and 24 hours after the start of each trial. Each experiment had a control treatment that consisted of prey species without a dytiscid predator to account for background prey mortality and predation.

Mortality in the control aquarium was subtracted from the number of prey consumed in the predator treatment.

Statistical analyses

Dytiscid feeding preference was determined using Rodger's preference score equation (Krebs 1998), which calculates the cumulative proportion of each species consumed over time relativized by the species with the maximum cumulative proportion eaten within the experiment. The preferences are only meaningful compared within the experiment because of the different combinations of prey offered. The Rodger's preference scores were compared for each experiment using a two-way ANOVA in which species and sex were fixed factors. Within treatment differences were determined with Tukey HSD comparisons. Statistical analyses were conducted using R software (R Development Core Team 2007).

Results

Field experiment

The limnological variables were similar across mesocosm treatments and ponds except for dissolved oxygen and temperature; MANOVA showed borderline significant treatment effects (F = 2.3, df = 2,15; *P* = 0.058). Dissolved oxygen levels in the ponds were significantly higher (7.8 ± 1.2 mg L-1) than the control mesocosms (6.5 ± 0.6 mg L-1) (F = 4.1, df = 2,15; *P* = 0.037). The ponds (18.1 ± 0.5 ºC) were also significantly warmer than the mesocosms (17.3 ± 0.4 ºC) (F = 6.0, df = 2,15; *P* = 0.012).

Mesocosms with *D. alaskanus* had significantly lower total macroinvertebrate biomass (Figure 1a) and predatory macroinvertebrate biomass (Figure 1b). The linear mixed effects model found significant treatment effects on macroinvertebrate biomass (F=10.4, df=53, *P*=0.0022) and predatory macroinvertebrate biomass (F=11.1, df=53, *P*=0.0016). Dytiscids had no significant effect on macroinvertebrate taxa richness (F = 2.2, df=53, P = 0.1465; Figure 1c). The dytiscid enclosures had lower biomass for the following taxa: *Gammarus lacustris* (4X), Hirudinea (4X), Corixidae (2X), Zygoptera (2X), *Chaoborus* sp. (1.5X), and Gastropoda (*Physa* sp., Planorbidae, *Promenetus umbilicatellus* (Cockerell, 1887), *Gyraulus* sp., *Menetus opercula* Gould, and *Armiger crista* L.) (1.5X) (see Table 1). The only macroinvertebrate with higher biomass in the presence of *D. alaskanus* was *Hyallela azteca* (2X higher biomass) (Table 1).

Zooplankton biomass was significantly higher in the dytiscid treatment enclosures (F = 9.5, df=53, *P* = 0.0032; Figure 1d) as was zooplankton species richness (F = 21.1, df=53, *P* < 0.0001; Figure 1e). Zooplankton biomass was significantly higher in dytiscid mesocosms, which was largely driven by an increased abundance of large and small Cladoceras (Table 1). Large Cladoceras (*Daphnia dentifera, D. pulex,* and *Simocephalus vetulus*) doubled their biomass in the presence of dytiscids, as did small Cladoceras (principally *Ceriodaphnia quadrangula* and *Chydorus sphaericus*). Other zooplankton groups including cyclopoids, calanoids, rotifers and ostracods showed no response to the treatments (Table 1).

There was no significant effect of dytiscids on phytoplankton biomass (F = 0.1, df=53, *P* = 0.8177; Figure 1f).

Periphyton biomass was significantly higher (6X greater) in the dytiscid enclosures compared to the control treatments (Figure 2). The linear mixed effects model found significant differences in periphyton total pigment concentrations between treatments (F = 9.4, df = 17, P = 0.0071).

Feeding preference laboratory experiments

In feeding preference experiments 1 and 2 the preferred prey of adult *Dytiscus alaskanus* was gastropods (*Physa* sp.) (Figure 3a, b). Large mobile macroinvertebrates such as Corixidae and Zygoptera (Figure 3a) and Trichoptera (Figure 3b) were secondary preferences of *D. alaskanus*. Ephemeroptera, *Gammarus lacustris*, and *Hyallela azteca* were consumed in lesser quantities, while small invertebrates such as *Daphnia* sp. and Hydrachnidia were largely avoided. Dytiscids had significant preferences for prey species in experiments one (F value = 17.9, df = 4, P < 0.0001) and two (F value = 18.6, df = 5, P < 0.0001), however dytiscid sex had no effect.

In experiment 3, both *Chaoborus* and Corixidae were highly selected, while *Daphnia* was completely avoided. The two-way ANOVA model showed significant prey effects (F value = 32.7, df = 2, P < 0.0001). Dytiscid sex had no significant effect on prey preference (F = 0.2, df = 1, P=0.301), however there was a significant interaction between prey and sex; male dytiscids selected Corixidae significantly more than female dytiscids (df = 2, F = 7.1, P = 0.009) (Figure 3c).

In the fourth experiment dytiscids exhibited no feeding preference for either amphipod species (F value = 0.7, df = 1, P = 0.42).

Discussion

Dytiscid predation caused trophic effects via two distinct food chains - the benthic and the pelagic food chains (Figure 4). The benthic trophic cascade had three levels whereby *Dytiscus alaskanus* reduced the biomass of algivorous snails and other herbivores leading to increased production of periphyton. The pelagic food chain involved a partial trophic cascade with *D. alaskanus'* foraging on other predatory macroinvertebrates such as corixids, *Chaoborus*, and Zygoptera leading to increased zooplankton grazers; however, zooplankton grazing did not affect phytoplankton biomass.

Trophic cascade effects: Dytiscid – snail – periphyton

D. alaskanus predation of snails and other grazers led indirectly to increased periphyton biomass to cause a community level trophic cascade. Other predator macroinvertebrates likely contributed to this food chain effect; however, these impacts would have lessened over the course of the experiment as dytiscids preyed on the other predatory macroinvertebrates.

Other studies have found predatory macroinvertebrates capable of precipitating a trophic cascade effect on periphyton. Stav et al. (2000) observed a dragonfly larvae – mosquito – periphyton cascade, and Blaustein et al. (1995) observed a *Notonecta* – mosquito larvae – periphyton cascade. Dragonfly larvae and Hemiptera (*Belostoma flumineum*) negatively affect snail biomass and density (Turner et al. 2007), although trophic cascades were not documented in these studies. Fish-invertebrate-periphyton relationships have been observed from surveys of shallow lakes in the United Kingdom (Jones et al. 2003) and studies have documented fish (Bronmark et al. 1992; Bronmark 1994) and crayfish (Lodge et al. 1994) predation of snails that led to increases in periphyton.

Gastropods are key players in benthic systems and are the preferred prey of many large predatory insects including adult dytiscids, dragonfly nymphs, and the hemipteran *Belostoma flumineum* (Say), but not larval dytiscids (*D. verticalis* Say) (Turner et al. 2007). Gastropods were the preferred prey in the laboratory experiment. However, in the field experiment we observed greater reductions in the biomass of *Gammarus lacustris* and *Chaoborus.* These differences were likely due to the diversity of gastropod species present in the field experiment. In the laboratory experiments we offered only *Physa* sp., which is a thin-shelled gastropod. Snail species are known to vary in their shells' resistance to crushing, which alters their vulnerability to predators (Rundle et al. 2001). In contrast, there was a diverse gastropod species assemblage in the field experiment and treatment differences suggest that *Dytiscus alaskanus* consumed gastropod species differentially – *Physa* sp. was 5X higher in the control treatment compared to the dytiscid treatment, followed by *Armiger crista* (3X), and *Gyraulus* sp. (2X), while *Menetus opercularis* and *Promentus umbilicatellus* biomass did not differ between treatments (unpublished data). Thus dytiscids appear to prey preferentially on gastropod species and likely influence their abundance in ponds.

Trophic cascade effects: Dytiscid – predatory macroinvertebrates – zooplankton

Dytiscids caused a second trophic cascade effect via the consumption of predatory macroinvertebrates, including *Chaoborus* sp., Corixidae, and Zygoptera, which reduced grazing pressure on zooplankton. The laboratory experiments confirmed that in addition to gastropods, *Dytiscus alaskanus* preferred prey were large mobile predaceous macroinvertebrates including Corixidae, Zygoptera and *Chaoborus*. *Daphnia* was not consumed by *D. alaskanus* in the laboratory experiments. Other adult dytiscid species (*Cybister fimbriolatus fimbriolatus* and *Ilybius discedens*) similarly do not consume *Daphnia* (Johnson and Jakinovich 1970; Hicks 1994), whereas *Daphnia* do form small proportions of the diet of others (Kehl and Dettner 2003, Hicks 1994). Other predaceous macroinvertebrates have been shown to directly reduce zooplankton abundance and biomass including *Notonecta* (Shurin 2000; Arnér et al. 1998), *Chaoborus* (Vanni and Findlay 1990) and odonates (Burks et al. 2001). Uniquely, this study showed dytiscids precipitated an indirect top-down effect whereby consumption of predaceous macroinvertebrates led to an increase in zooplankton biomass.

Dytiscids did not precipitate a trophic effect via zooplankton to phytoplankton. According to food web theory, high densities of large-bodied grazing zooplankton, such as *Daphnia pulex, D. dentifera* and *Simocephalus* that were common in these ponds, would be expected to suppress phytoplankton biomass. Macroinvertebrate predators may be less likely to cause a trophic cascade effect on phytoplankton compared to fish (Vanni and Findlay 1990). This study contributes to a growing body of research on macroinvertebrate predators that indicates top-down control of zooplankton does not lead to effects on phytoplankton. Vanni and Findlay (1990) that found that fish and *Chaoborus* had similar predatory effects on *Daphnia* but these trophic effects only cascaded down the food chain to phytoplankton in the presence of fish. They postulated that *Chaoborus* retained phosphorus from their prey thus limiting phosphorus available for uptake and growth by phytoplankton, whereas fish have high phosphorus excretion rates that promotes phytoplankton growth resulting in a trophic cascade. Shurin (2000) also found that *Notonecta* predator effects on zooplankton did not extend to phytoplankton. However, Arnér et al. (1998) did observe *Notonecta* trophic cascade effects via mosquito larvae to phytoplankton.

Zooplankton biomass and species richness were higher in the presence of dytiscids. Previous studies have observed a positive correlation between zooplankton biomass and species diversity (Dodson et al. 2000; Hessen et al. 2006). As the abundance of zooplankton increases so may the occurrence of rare species. In contrast, dytiscids had no significant effect on macroinvertebrate taxa richness, which suggests that predation pressure by dytiscids was insufficient to cause local extinctions of specific taxa, at least within the time frame of the study.

Top-down trophic cascades are rarely observed in mesotrophic to eutrophic systems, which suggests that phytoplankton is typically driven by bottom-up forces. When zooplankton density was increased in a mesotrophic lake, total phytoplankton biomass showed an insignificant response (Sommer et al. 2003). Similarly, Proulx et al. (1996) found that phytoplankton biomass increased with nutrient additions (bottom-up control), but not with the addition of fish (top-down control) in an mesotrophic lake. In tropical flood plain lakes zooplankton were mainly top-down controlled whereas phytoplankton were bottom-up controlled (Rejas et al. 2005).

Trophic cascade effects: synthesis

Fishless boreal ponds are rife with diversity and other factors predicted to reduce the effects of trophic cascades including interspecific competition, omnivory, and spatial and temporal heterogeneity (Strong 1992). The macroinvertebrate and zooplankton communities were species rich which according to trophic cascade theory would be expected to have dissipated trophic effects. Other attributes of the boreal pond communities are consistent with trophic cascades predicted by Strong (1992) – the conditions are mesotrophic with periphytic algae at the base of the food web that is vulnerable to herbivory.

However, the consumption patterns of the invertebrate communities appear unified and thus trophic effects were strong despite the high species richness.

Gastropods and other grazers collectively consumed periphyton. Similarly, the macroinvertebrate predator community collectively appears to have targeted small and large species of Cladoceras, leading to a trophic level effect. This study provides further evidence that trophic interactions can be important in structuring freshwater littoral food webs despite their high diversity and tangled food webs (Bronmark 1994; Bronmark et al. 1997; Nystrom et al. 2001; Jones et al. 2003).

Implications for fishless pond ecosystems

Manipulating the density of top predators in mesocosm field experiments has clear advantages such as ease of replication and experimental controls. We endeavoured to maximize the generality of the results by conducting the field experiment in six boreal fishless ponds with a range of macroinvertebrate species richness, community composition and biomass. Yet mesocosm studies have many problems that limit the applicability of the results to the natural pond ecosystem including: short duration, small size, reduced spatial and temporal variability, reduced exchange with the lake, and are subject to edge effects relative to the ponds they are attempting to mimic. The temperature and dissolved oxygen levels were lower in the mesocoms compared to the ponds indicating that the mesocosms were partially shaded and the water more stagnant. Enclosures are also known to limit the immigration of algae (e.g., (Swamikannu et al. 1989) and other aquatic organisms. As well, enclosing the predator and prey in a confined space limits the prey's ability to avoid the predator. Prey in fishless permanent ponds are highly mobile and use their mobility as a predator avoidance tactic

(Wellborn et al. 1996). Despite these limitations, this study shows that dytiscids are capable of forcing a trophic cascade in a variety of species-rich ponds.

Tables

Table 2-1. Descriptive summary statistics of the macroinvertebrate and zooplankton responses to the mesocosm treatments over the course of the experiment (weeks 2 - 6).

	Treatment			
	Dytiscid (n=12)		Control (n=12)	
Taxa	Mean biomass (µg L-1)	Standard error (µg L-1)	Mean biomass (µg L-1)	Standard error (µg L-1)
Total macroinvertebrates	1331.1	3405.4	1461.7	1803
Predatory macroinvertebrates	205.9	288.9	381.1	366.5
Hyallela azteca	852	3353.1	391.8	1456.8
Gammarus lacustris	143.1	328.3	525.4	1089.4
Chaoborus sp.	94.2	172.2	145.9	258.85
Gastropoda	56.7	190.4	85.9	247.2
Corixidae	44	88.8	91.4	132.9
Hirudinea	24.2	49.2	85.2	174.5
Bivalvia	29.6	143.7	31	82.8
Zygoptera	15.9	63.4	27.1	70
Hemiptera other	15.4	59.4	20.2	83.4
Hydrachnidia	14.8	31.3	20	40.7
Diptera other	14.4	26.1	14.1	28.5
Coleoptera	9.5	19.7	9.4	15.9
Trichoptera	6	28.8	3.6	10.7
Ephemeroptera	1.8	4.5	2.6	5.9
Other miscellaneous taxa	9.4	28.7	8	20
Total zooplankton	1276.8	1387.1	840.3	1136
Large Cladoceras	674.3	725.4	327.6	324.4
Rotifers	290.8	791.5	248.6	902.6
Calanoids	106	128.9	78	103
Small Cladoceras	113.9	176.6	59.6	97
Cyclopoids	56.8	67.1	71.9	117.2
Ostracoda	33.2	56.3	51.5	170.8
Copepod nauplii	2.8	4.3	3.2	5.2
Harpacticoida	0.3	1.4	0.6	2.8

Figures

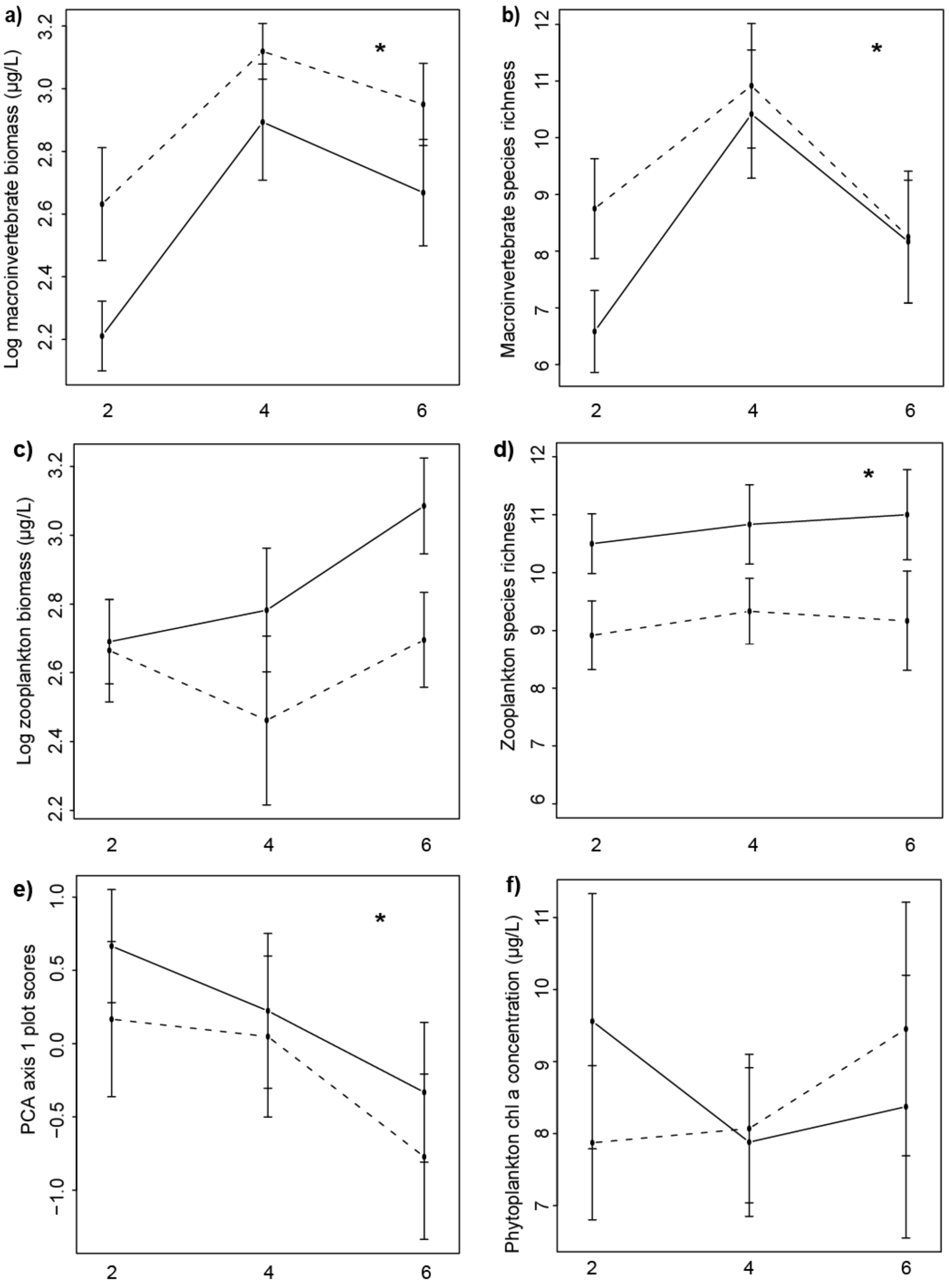

Figure 2-1. Mean values (± SE) of response variables to dytiscid treatments (black line) and control treatments (dashed line) sampled at 2, 4 and 6 weeks. Response variables were: a) total macroinvertebrate biomass, (b) predatory macroinvertebrate biomass, (c) macroinvertebrate species richness, (d) total zooplankton biomass, (e) zooplankton species

richness, and (f) phytoplankton biomass. Asterisks indicate significance at the Bonferroni-corrected critical value of *P* < 0.008.

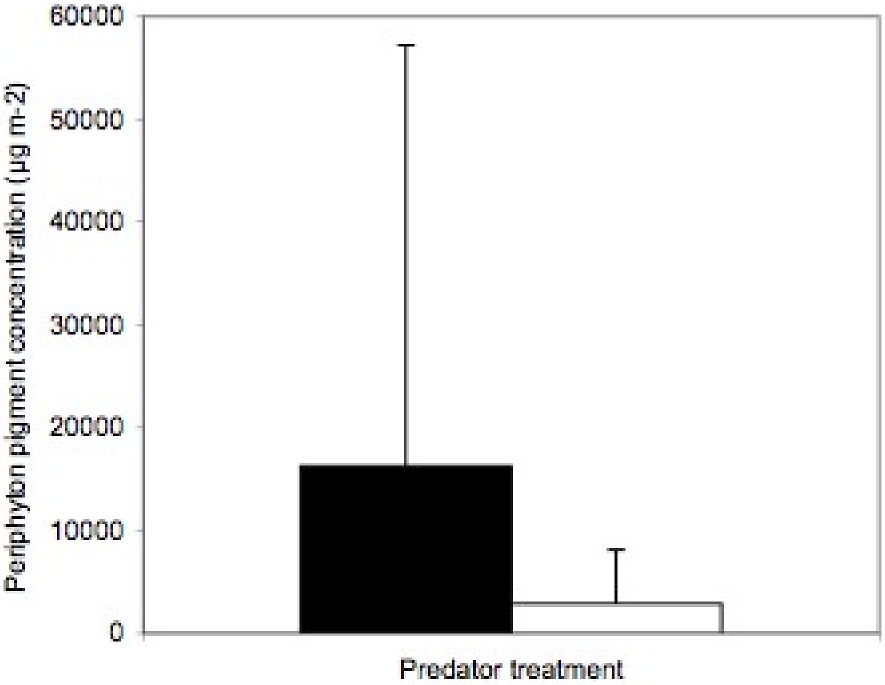

Figure 2-2. Means of periphyton pigment concentration (± SE) for dytiscid (black bars) and control (white bars) treatments.

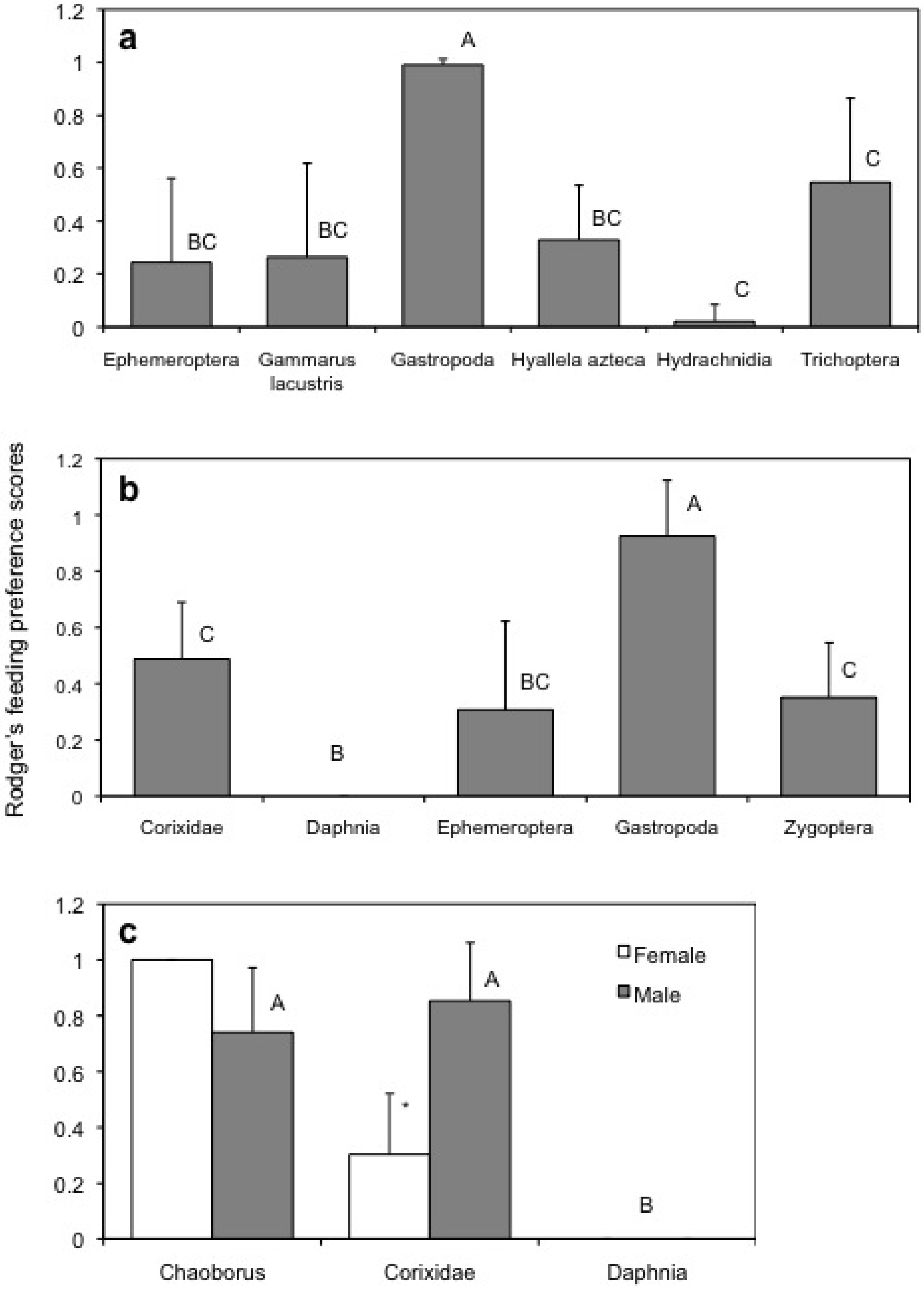

Figure 2-3. Means of feeding preference scores (±SE) in laboratory experiment a) #1, b) #2, and c) #3. Different letters represent significant differences in prey taxa identified with a Tukey test. The asterisk represents a significant interaction between prey and sex identified with a Tukey test.

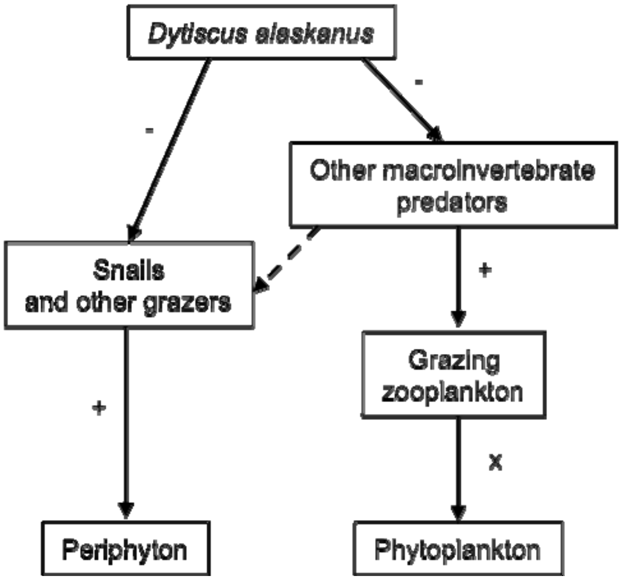

Figure 2-4. Diagram of trophic interactions observed in fishless boreal pond communities. Dytiscid predation of snails and other grazers led to increased periphyton; other predatory macroinvertebrates likely facilitated the consumption of the herbivores (dashed line). Dytiscid consumption of other predatory macroinvertebrates led to increased abundance of zooplankton. No top-down effects of dytiscids were detected for phytoplankton abundance. + or – indicates whether the interaction is positive or negative and the x indicates no effect.

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Chapter 3 – **Lake and landscape factors affecting the persistence of alternative regimes in shallow lakes of the Boreal Plains (Alberta, Canada)**

Introduction

Shallow lakes are widely regarded as a classic example of ecosystems exhibiting alternative regimes (Scheffer et al. 1993; Carpenter et al. 1999; Chase 2003). One regime is dominated by submersed aquatic vegetation (SAV) with clear water at low total phosphorus (TP) concentrations, and the other regime is dominated by phytoplankton with high turbidity at high TP concentrations, but at intermediate phosphorus concentrations either state may exist. Typically, shifts between alternative regimes occur only occasionally following strong perturbations (Scheffer et al. 2001). However, a recent study from Bayley *et al.* (2007) found that the majority of lakes in the Boreal Plains, Alberta, Canada had highly unstable alternative regimes, with 73% switching 2-9 times over a 20-year period. The high frequency of switches in a relatively pristine environment suggests that small perturbations in climate are important in driving the switches and the mechanisms that maintain the clear or turbid regimes are weak (i.e. the regimes lack resilience). This study investigates the positive feedback mechanisms that help maintain alternative regimes in shallow lakes, and the lake and landscape attributes that affect the persistence of alternative regimes in shallow lakes on the Boreal Plains.

Switches between alternative regimes are often induced by an external forcing factor, such as eutrophication or a change in lake level, but the persistence of each regime may be reinforced (stabilized) by internal positive feedback mechanisms (Moss 1990; Scheffer et al. 1993). SAV provides structure to shallow lakes that clearly differentiates the clear and turbid water regimes (Moss 1990). Macrophytes help maintain the clear water regime by reducing sediment resuspension (Barko et al. 1998), providing a predation refuge for zooplankton that graze on phytoplankton (Burks et al. 2002), and promoting piscivore control of planktivorous fish (Blindow et al. 1993). Perennial vegetative structures enable growth the following year further maintaining the state from year-to-year (Jeppesen et al. 1997). In contrast, when the same lakes may have high concentrations of nutrients, a phytoplankton-rich regime may be equally resilient. Phytoplankton blooms appear to competitively exclude macrophytes through rapid nutrient uptake and re-release of phosphorus leading to algal blooms and shading (Jeppesen et al. 1997; Scheffer 1998). Phytoplankton grows much earlier in the season than aquatic plants and may hamper the growth of turions and seeds early in the spring (Moss 1990). Planktivorous fish promote phytoplankton growth through the consumption of zooplankton, and rapidly recycling nutrients. Fish and waves also stir up sediments when there is no vegetation present promoting internal phosphorus loading. Light limitation due to algae blooms and disturbance of the sediments make it difficult for vegetation to establish (Jeppesen et al. 1997; Jeppesen et al. 1998; Scheffer 1998; Moss 2010).

The rapid and repeated regime shifts observed in shallow lakes on the Boreal Plains (Bayley et al. 2007) suggests that internal mechanisms that maintain alternative regimes in other shallow lake systems may be weak or lacking. Top-down effects mediated by fish play a central role in maintaining alternative regimes in the initial model of Scheffer et al. (1993). However, shallow lakes on the Boreal Plains are mainly fishless. Brook stickleback (*Culaea inconstans* Kirtland) is the only fish observed in these shallow lakes (Norlin et al. 2005; Hornung et al. 2006; Norlin et al. 2006), which often experience winter hypoxia that leads to mortality ('winterkill') of less tolerant fish (Conlon 2002; Tonn et al. 2004). Large predatory macroinvertebrates are top predators in shallow fishless lakes where they are abundant and diverse compared to fish bearing water bodies (Mallory et al. 1994; Batzer et al. 1996; Wellborn et al. 1996; Tonn et al. 2004; Hornung et al. 2006). Few studies have examined the importance of food web structure in maintaining alternative regimes in primarily fishless shallow lakes. Predatory invertebrates are a critical factor affecting the species composition of prey communities in shallow fishless waterbodies (Wellborn et al. 1996). Invertebrate predators are capable of causing trophic cascade effects via consumption of zooplankton to phytoplankton (Arner et al. 1998), and via macroinvertebrate grazers to periphyton (Blaustein et al. 1995; Stav et al. 2000). Evidence suggests that macroinvertebrate grazers may have an important role in suppressing epiphyton and maintaining high macrophyte biomass in clear water lakes (Jones et al. 2003). I hypothesized that the SAV-rich regime would be associated with fishless lakes with a rich macroinvertebrate community that suppresses epiphyton. In contrast, the phytoplankton-rich regime would be associated with fish-bearing lakes with reduced zooplankton grazers and increased phytoplankton biomass, consistent with the initial model of Scheffer et al. (1993).

I was interested in how spatial variability in lake features would affect the persistence of alternative regimes to regional changes in climate (the primary disturbance affecting the study region) over time. A lake district is a landscape rich in lakes that share a common origin, climate, and catchment geology. Yet despite these common features, lakes within a district vary considerably in their physical, chemical and biological characteristics. Lake features ranging from internal features such as food web structure and nutrient cycling to morphometry and the interaction between a lake and its catchment may be the cause of spatial variability within a district.

Lakes on the Boreal Plains are sensitive to fluctuations in inter-annual precipitation due to constraints imposed by the climate and landscape. The relatively flat topography, glacially derived sediments, and sub-humid climate produce low runoff (Redding and Devito 2008). The lakes are small, shallow, and isolated. The hydrologic budgets of a moraine lake and lowland organic lake were dominated by precipitation inputs (83 – 95%) and evaporative outputs (93 – 96%). Lateral groundwater exchange between the surrounding peatlands and the lakes constituting the remainder of the water fluxes, with negligible surface water runoff (< 1%) (Ferone et al. 2004). Evaporative concentration of nutrients and organic matter in isolated lakes is an important mechanism influencing phytoplankton production, as seen in other boreal lakes (Schindler et al. 1996), in Lake Vortsjarv, a large shallow lake in Estonia (Noges et al. 1999) and several floodplain lakes (Sokal et al. 2008; Loverde-Oliveira et al. 2009; McGowan et al. 2011). Shallow groundwater inputs from adjacent peatlands can be important source of water and phosphorus to shallow lakes on the Boreal Plains (Ferone et al. 2004). Drought conditions are attenuated in lakes connected to large peatlands due to shallow groundwater flow reversals (Ferone et al. 2004).

Lake position in the landscape can also affect a lake's sensitivity to drought. In northern Wisconsin, precipitation and transient inputs of local groundwater flow dominate the hydrologic budget of seepage lakes high in the landscape, which lack surface water inlets and outlets, and thus tend to be low in ionic strength. Lowland lakes receive groundwater discharge from deeper regional flowpaths that have longer contact times for weathering reactions with minerals in the aquifer and thus, higher solute concentrations (Kratz et al. 1997). Lakes higher in the landscape were shown to respond more strongly and recover more slowly to drought than lakes lower in the landscape (Webster et al. 2000).

Heterogeneity of surficial geology types may regulate patterns of some lake response variables and dynamics on the Boreal Plains. Topography is generally a poor predictor of soil moisture distribution and run-off responses on the Boreal Plains (Devito et al. 2005). Spatial variability may be better defined by surficial glacial deposit types (e.g. sand outwash, clay-silt moraines, and peat-covered low-lying lacustrine clay) than topographic catchments (Devito et al. 2005). Variations in surficial geology deposits affect water storage, runoff, and fluxes of solutes and nutrients from groundwater and surface water sources (Devito et al. 2000; Devito et al. 2005). Differences in bedrock geology had strong influences on spatial gradients of some limnological variables on Shield bedrock in south-central Ontario, Canada (Quinlan et al. 2003).

I hypothesized that the persistence of alternative regimes to inter-annual changes in precipitation would depend on a lake's relative sensitivity to drought. The SAV-rich regime would be more persistent in lakes that were resistant to drought, whereas the phytoplankton-rich regime would be more persistent in lakes that were more sensitive to drought. Lake sensitivity to drought was predicted to increase with decreasing lake size and maximum depth (Wolfe et al. 2007), increasing elevation in the landscape (Webster et al. 2000), decreasing groundwater connectivity (Kratz et al. 1997), and decreasing shallow ground water connection with adjacent peatlands (Ferone et al. 2004). Finally, the heterogeneity of surficial geology types (glaciofluvial > morainal > organic) may affect a lake's sensitivity to drought through the integration of landscape features such as lake position, extent of wetlands in the buffer, and/ or lake morphometry.

The study is based on a survey of 23 lakes on the Boreal Plains, Alberta, Canada monitored from 2001 to 2007. The first objective was to determine the internal feedback mechanisms that are helping to stabilize alternative regimes in shallow lakes on the Boreal Plains. The lakes were classified as SAV-rich or SAV-poor, and phytoplankton-rich or phytoplankton-poor using previously established thresholds. This study expands on the work of Bayley and Prather (2003) and Bayley *et al.* (2007) by examining the biotic communities in more detail over a longer time. I focused on food web interactions to determine whether the predominantly fishless communities of shallow lakes on the Boreal Plains may have fewer internal feedback mechanisms to maintain the alternative regimes.

The second objective was to determine the lake and landscape features that best predict the persistence of the alternative regimes in shallow lakes on the Boreal Plains. Regime persistence was the percentage of time that each lake was dominated by SAV and phytoplankton from 2001 to 2007. We tested key lake-variables identified from the first objective (maximum lake depth, standard deviation of lake depth, TP, dominance of *Daphnia* within the Cladocera community, macroinvertebrate predator biomass, and fish prevalence) and key landscape variables (lake elevation, surface water connectivity, groundwater connectivity, wetland extent and dominant surficial geology type in local catchment, and lake area) to determine the best predictors of alternative regime persistence using regression tree analysis. Understanding whether landscape attributes can be relied on to predict lake conditions and dynamics is a priority for addressing environmental issues at regional scales (Vitousek 1994).

Materials and Methods

The ecosystem

The study area is located approximately 370 km north of Edmonton, Alberta, Canada (56°6 N, 116 º32' W; Figure 3-1). The study area is part of the Boreal Plain ecozone of the Western Boreal Forest (extending across three provinces in west-central Canada), approximately 150 km south of the discontinuous permafrost zone (Woo et al. 1993). Long cold winters and short warm summers characterize the climate with average monthly temperatures ranging from -14.5 to 15.6 ºC for a mean annual temperature of 1.7ºC (Environment Canada 2003). The long-term (1971 – 2007) average annual precipitation is 466 mm, of which 59% falls during the growing season.

The terrain of the Boreal Plains has low relief and is composed of rolling moraines, low-lying clay plains and coarse textured outwash areas. Extensive peatlands and shallow lakes occur in low-lying areas, which are interspersed by upland areas dominated by trembling aspen (*Populus tremuloides* Michx.). The surficial geology consists of glacially derived sediments varying from 40 to 240 m thick (Pawlowicz et al. 2002) overlying marine shales of the Upper Cretaceous Smoky Group (Hamilton et al. 1999). There are three surficial geology types in the study area including 1) glaciofluvial deposits, which are comprised of coarser sediments such as sand; 2) morainal deposits, which are comprised of finer sediments such as silt and clay; and 3) organic deposits that tend to overlie glaciolacustrine plains comprised of fine clay sediments (Alberta Geological Survey 2004).

The 23 study lakes were distributed along a 45 km transect selected from a spanning the surficial geology types in the region. The lakes were selected in a stratified random design such that there were approximately an equal number of lakes on each of the surficial geology types. There were seven lakes on the glaciofluvial deposits, eight on the morainal deposits, and eight on the organic deposits. The lakes were small, ranging from 0.9 ha to 44.5 ha (mean ± stdev;

10.9 ± 12.1 ha), and shallow with flat bottoms. Average water depths ranging from 28 cm to 213 cm (83 ± 34 cm). The lakes are naturally mesotrophic with moderate concentrations of total phosphorus (median = 59.7 µg TP L^{-1}; 12.4 – 670.4 µg TP L^{-1}), nitrogen (median = 1990 µg TN L^{-1}; 618 – 5230 µg TN L^{-1}) and dissolved organic carbon (median = 39.5 mg DOC L^{-1}; 16.8 – 705.1 mg DOC L^{-1}) (Bayley et al. 2007). The water was typically phosphorus-limited with average total nitrogen to total phosphorus mass ratio of 17:1, and average available nitrogen to phosphorus ratio of 34:1 ([ammonium + nitrite-nitrate]: soluble reactive phosphorus).

Algae grew quickly after ice-out and submerged macrophytes typically reach peak biomass in early August. Common primary producers included cyanobacteria (primarily Chroococcales, *Microcystis* spp. and Nostocales) and green algae (Chlorophyta), floating duckweeds (*Lemna minor* L. and *Spirodela polyrhiza* (L.) Schleid.) and submerged macrophytes (primarily *Myriophyllum sibiricum* Kom., *Ceratophyllum demersum* L., *Potamogeton friesii* Rupr., *P. richardsonii* (A. Benn.) Rydb., and *P. zosteriformis* Fern..

The zooplankton community was composed primarily of Cladocera (64%) and copepods (36%). The dominant Cladocera are *Daphnia dentifera* Forbes 1893 (formerly *D. rosea* G. O. Sars, 1862 (Taylor et al. 1996)) (32% of the Cladocera), *D. pulex* Leydig, 1860 (10%), *Chydorus sphaericus* (O. F. Mueller, 1785) (20%), *Ceriodaphnia quadrangula* (O. F. Müller, 1785) (19%), *Simocephalus vetulus* (O. F. Müller, 1776) (9%), *Diaphanosoma birgei* Korinek, 1981 (4%), *Bosmina longirostris* (O. F. Müller, 1776) (4%), and *Polyphemus pediculus* (Linnaeus,

1761) (2%). The dominant copepods were *Skistodiaptomus oregonensis* (Lilljeborg in Guerne and Richard, 1889) (18% of copepods), *Macrocyclops albidus* (Jurine, 1820) (12%), and *Eucyclops agilis* (Koch, 1838) (3%). A list of zooplankton taxa and biomass is presented in Appendix A.

The macroinvertebrate community was dominated by Amphipoda (39%) – primarily *Hyallela azteca* (Saussure) and *Gammarus lacustris* (Sars), Gastropoda (22%) including *Lymnaea stagnalis* (Linnaeus), *Stagnicola* spp. and *Physa* spp., Coleoptera (9%) primarily *Dytiscus* alaskanus J. Balfour-Browne, 1944; Hirudinae (6%) including *Nephelopsis obscura* (Verrill, 1872), *Placobdella ornata* (Verrill, 1872), and *Erpobdella punctata* (Leidy)), Odonata (5%) including *Libellula* sp., *Sympetrum* sp., *Leucorrhinia* sp.), Hemiptera (5%) including *Notonecta* sp., *Somatochlora* sp., and *Sigara* sp., Tricoptera (5%) primarily *Triaenodes* sp. and *Ptilostomis* sp., Bivalvia (4%) primarily Sphaeriidae, and Diptera (4%) including Chironomidae and Chaoboridae. A list of macroinvertebrate taxa, feeding guilds, and biomass is presented in Appendix B.

During the study period, 18 of the lakes lacked fish. Brook stickleback were observed in three of the lakes during all seven years, one lake in five years, and one lake in one year.

Lake survey

A survey of 23 lakes was conducted early – mid August during peak biomass of SAV from 2001 to 2007. Physical conditions, water chemistry and phytoplankton biomass (chl-*a*) were sampled from three sites (nearshore, mid-width and centre) and pooled to estimate the overall lake conditions, unless otherwise stated. Temperature, pH, dissolved oxygen, and electrical conductivity were measured in the field using a Hydrolab Quanta field probe (Hydrolab Corporation, Austin, Texas, U.S.A.). Physical factors measured included average water depth (typically n = 15), Secchi disk depth and turbidity. Turbidity was measured in the field using a Turner Designs Aquaflor Turbidimeter, which was calibrated with laboratory measurements. The water chemistry samples were collected with an integrated sampling tube, stored in dark bottles and kept cool (4º C) until they could be processed in the lab within 8 hours of collection. Water chemistry analyses were conducted at the Biogeochemical Laboratory at the University of Alberta following standardized procedures as described in Bayley and Prather (2003) for the following variables: phosphorus ([TP], total dissolved phosphorus [TDP], soluble reactive phosphorus [SRP]), nitrogen (total nitrogen [TN], total inorganic nitrogen [TIN], nitrate-nitrogen [NO_3^-], and ammonium-nitrogen [NH_4^+]), dissolved organic carbon [DOC], anions (chloride [Cl], sulphate [SO4]) and cations (sodium [Na], potassium [K], calcium [Ca], magnesium [Mg], iron [Fe] and silica [Si]). Chl-a was extracted with 95% ethanol and analysed with a spectrophotometer at 750, 665, and 649 nm (Bergmann et al. 1980).

SAV cover was estimated in each lake from 2001 to 2007. An overall lake assessment was based on 10 - 20 random quadrats (1 m^2). We used a ranked scale that ranged from 1 to 5, where S1 = little to no SAV cover (< 0.05%), S2 = sparse SAV cover (0.05 - < 5%), S3 = occasional plant cover (5 – < 25 %), S4 = common SAV cover (25 – < 75 %) and abundant SAV cover (75 –100 %). This ranked scale was developed for aerial surveys of SAV coverage of shallow lakes in the region (Bayley et al. 2003; Bayley et al. 2007) and continued in this study. The ranking included only SAV and excluded floating and emergent vegetation which formed only a minor proportion of vegetation biomass and cover (personal observation). SAV biomass was sampled in each of the lakes from 2001 to 2004. We sampled SAV biomass using standardized rakes (1.00 x 0.38 m) from 20 random quadrats (1 m^2). The SAV biomass was stored in paper bags and dried at 65º C to constant weight (approximately 5 days). Regression analysis showed SAV cover ranks provide a reasonable and practical proxy for biomass in these lakes ($R^2 = 0.77$, $p < 0.0001$, $n = 24$ lakes) (Bayley et al. 2007).

Phytoplankton samples were collected from three sites (nearshore, mid-width and centre) with an acrylic tube (135 cm length x 6.5 cm diameter) and pooled in a 20L pail. After mixing thoroughly, a 400-mL subsample was stored in a dark bottle and preserved with 50mL of FAA (formalin: acetic acid: ethyl alcohol). Algal cells were counted using an inverted microscope at 400 X magnification in Utermöhl chambers (Lund et al. 1958). Phytoplankton community structure was defined based on the concentration (number of cells per nanolitre) of 14 different taxonomic groups as outlined in Norlin et al. (2005).

Zooplankton samples (2 L) were collected with an acrylic tube (135 cm x 6.5 cm) (Swanson 1978), passed through 64-µm mesh netting, and preserved with a 4% formalin-sugar solution (Prepas 1978). We enumerated several subsamples, such that ~ 400 individuals were counted per total sample. Subsamples were obtained with a wide-bore trigger pipette and identified using a counting wheel with a Wild M5 (40X magnification) dissecting scope (Wild Heerbrugg, Switzerland). Zooplankton adults were identified to genus or species using Thorp and Covich (2001) or Edmondson (1959). Zooplankton body length was categorized into four length classes (0.63 - 0.9 mm, 0.9 - 1.45 m, 1.45 - 2.05 mm and more than 2.05 mm). Numbers were converted to biomass using the length-weight regressions of McCauley (1984).

Macroinvertebrates were sampled in all study lakes in 2001 and 2006 with two upward vertical sweeps with a standard D-shaped invertebrate dip net (640 cm^2 opening, 500 µm mesh size). Samples were chilled on ice and were sorted from vegetation within 8 hours of sampling and preserved in 70% ethanol. Macroinvertebrates were counted and identified to the lowest possible taxonomic resolution (Clifford 1991; Merritt et al. 1996; Thorp et al. 2001) and classified to feeding guild according to Merritt and Cummins (1996), Barbour et al. (1999) and Wiggins (1996) and Clifford (1991). All macroinvertebrate specimens were measured for wet weight and converted to dry weights using a reference collection of at least 30 individuals that were dried at 60° C and weighed to the nearest 0.0001g.

Fish presence/ absence (Brook stickleback, *Culea inconstans*) was determined using 10 to 20 Cuba Minnow Traps (Cuba Specialty Manufacturing, Fillmore, NY, U.S.A). The traps were placed at 5 to 10-m intervals in the outer margin of emergent shoreline and left for 24 hours in each lake, which corresponds to the greatest abundance of adults trapped in previous population studies of brook stickleback (Moodie 1986).

We determined periphyton biomass in 2006 using polyethelene strips, which approximates the biomass of periphyton on macrophytes (Brönmark et al. 1992). Two strips (46 cm length x 6 cm width) were suspended vertically on two stands that were placed on the lake bottom, resulting in four strips in each lake. The stands were placed in south-facing locations in 50 to 77 cm depth water. Average water depth of the stands on the start and end dates were obtained. The strips were installed from June 23-26, 2006 and retrieved approximately 6 weeks later from July 28-August 6, 2006. Periphyton on the strips was pooled and stored on ice for up to 4 hours until they could be processed in the laboratory. Periphyton was removed with razor blades, rinsed with water and adjusted to a fixed volume. Periphyton biomass was quantified using reversed-phase high-performance liquid chromatography (HPLC) using standard techniques (Leavitt et al. 1994) to estimate biomass and community composition. Periphyton biomass was normalized to account for differences in colonization time (assumed linear relationship) and average water depth (assumed vertical light attenuation with depth is exponential (Kalff 2002) among lakes.

Landscape attributes

GIS analysis was used to extract landscape information for each of the lakes using ArcGIS, version 9.2 (ESRI (Environmental Systems Research Institute) 2006). Lake area and perimeter were determined from SPOT imagery in 2009 (Province of Alberta 2010). Elevation was used as a metric of lake position within the regional flow path. However, elevation differences do not provide adequate information about the hydraulic gradient and the flow of water, or the scale of interaction among landscape units (Devito et al. 2005). Lake surface water connectivity was assessed using Strahler stream order derived from a hydrologically conditioned digital elevation model (DEM) (scale of 1:20,000). Lakes were assigned to three categories based on the presence or absence of inflow and outflow streams. Isolated lakes were unconnected to any permanent stream. Headwater lakes had an outflow stream only. Flow-through lakes were connected to an inflow and outflow stream. Lake connectivity with groundwater was estimated using the concentration of calcium and magnesium (Ca + Mg mg L^{-1}), which has been used to define the interactions of lakes with the groundwater flow system in northern Wisconsin (Webster et al. 1996; Kratz et al. 1997; Webster et al. 2000) and has been applied on the Boreal Plain (Devito et al. 2000; Sass et al. 2008).

The area within a 300m buffer around each lake was used to determine the local catchment variables contributing to the lakes, including the dominant surficial geology type (glaciofluvial, morainal or organic) (Alberta Geological Survey 2004; Alberta Geological Survey 2006), and the proportion of wetlands in the surrounding landscape based on Ducks Unlimited Canada's Enhanced Boreal Wetland Inventory (Ducks Unlimited Inc. 2004).

Data analysis

My first objective was to classify the alternative regimes of shallow lakes on the Boreal Plains. I used previously established thresholds for SAV dominance and phytoplankton dominance to define alternative regimes. SAV dominance was defined using a threshold value of 25% cover (SAV rating ≥ 3) based on previous studies in the region (Bayley et al. 2003). Shifts from clear to turbid regimes have been observed at similar threshold values, > 20% cover (Van Geest et al. 2007) and > 30% cover (Jeppesen et al. 1990), in other shallow lake systems. Phytoplankton dominance was identified using a threshold chl-*a* concentration of 18 µg/L based on previous classification and analyses (Bayley et al. 2007). We classified each lake for all the study years as SAV-rich or SAV-poor, and phytoplankton-rich or phytoplankton-poor. I could have used the SAV and phytoplankton thresholds to define four lake regimes: 1) SAV-rich and phytoplankton-poor, 2) SAV-poor and phytoplankton-rich, 3) SAV-poor and phytoplankton-poor, and 4) SAV-rich and phytoplankton-rich, for subsequent analyses similar to Bayley et al. (2003). However, my primary focus was to identify the effects of SAV and phytoplankton on the limnological conditions and biological communities. I identified these effects by comparing SAV-rich versus SAV-poor lakes, and phytoplankton-rich versus phytoplankton-poor lakes, in separate analyses.

I assessed whether the SAV-rich and SAV-poor regimes appeared to respond to changing environmental conditions with a pattern that was consistent with alternative stable state theory as recommended by Scheffer and Carpenter (2003) and followed by Bayley et al. (2007). First, I examined whether there was evidence for abrupt shifts between alternative regime through time. Second, I examined the frequency distribution of SAV coverage and chl-*a* concentration for evidence of bimodality. Finally, I characterized the relationships between the state variables and control variables including chl-*a* and TP concentration, turbidity and chl-*a*, and turbidity and SAV cover for clear and turbid lake groups using analysis of covariance (ANCOVA). I tested the data for the following models: (1) common slope and intercept for both turbid and clear lakes, (2) a common slope but separate intercepts for clear and turbid lakes, and (3) separate slopes and intercepts for clear and turbid lakes. A dualistic relationship (models 2 & 3) between the response and predictor variables is not proof of alternative regimes, but does support their existence (Bayley et al. 2007).

I then examined differences in the limnological conditions and biotic communities of the SAV-rich and SAV-poor lakes, and the phytoplankton-rich and phytoplankton-poor lakes. Differences between the alternative regimes for each lake for all years (n =161 for all lake-years during the study) were tested with t-tests if the data were normally distributed, or the Mann-Whitney U test for non-parametric data, or the chi-squared test for presence/ absence data (only fish). Raw and $\log_{10}(y+1)$ transformed data were tested for normality using the Shapiro-Wilk test. The '+1' was added to avoid problems with zero observations. I conducted multiple hypothesis tests because we were interested in summarizing key similarities and differences in the two groups of lakes. However, multiple testing means that as the number of tests increases, so does the probability of making a Type 1 error. To minimize our chances of making a Type 1 error I present the *p*-values and the Bonferroni procedure significance levels.

My second objective was to identify lake and landscape attributes associated with the persistence of SAV-rich and phytoplankton-rich regimes. I used regression tree analysis to describe the lake and landscape variables best predicting the persistence of the alternative regimes. Regression tree analysis is a non-parametric recursive technique that partitions data into homogeneous subsets with the smallest within-group variance for the response variable (De'Ath et al. 2000). It allows categorical and/ or numeric predictive variables. Regression tree analysis is an alternative to multiple linear regression analysis that is a flexible and robust method that can deal with nonlinear relationships, high-order interactions and missing values (De'Ath et al. 2000). All possible binary splits of the observations are assessed for each predictor variable. The first split is based on the predictor that results in two groups with the smallest within-group (residual) sums-of-squares for the response variable. This ‘recursive binary partitioning’ process is repeated within each of the two groups for each of the predictors until there is a minimum reduction in explained variance from adding more nodes. The variance explained by each of the splits is represented graphically by the relative lengths of vertical lines associated with each split. The *a priori* stopping criteria was that the within-node deviance must be at least 0.01 times that of the root node for the node to be further split. The total proportion of the sum of squares (variance explained) described by the model is presented. Small sample size (n = 23) prevented using a cross-validation approach to determine prediction error and the appropriate tree size as recommended by De’ath and Fabricius (2000). I used the *tree* package in R to develop the regression trees using the default settings (Ripley 2010).

Regime persistence was the average number of years that each lake was dominated by SAV and phytoplankton. I first tested key lake-specific variables based on results from objective one including: maximum lake depth, standard deviation of lake depth, TP, % *Daphnia*, macroinvertebrate predator biomass, and number of fish years. Lake variables were based on average values for the study period. I then tested landscape variables which may affect the persistence of the alternative regimes including: lake area, lake elevation as a metric of lake position in the landscape, Ca + Mg as a metric for groundwater connectivity, lake surface water connectivity based on Strahler stream order, and the dominant surficial geology type and wetland extent in local catchment. Finally, I tested which lake and landscape variables were the best predictors of alternative regime persistence.

Results

Classification of alternative regimes

Threshold values of SAV cover (> 25% cover = SAV-rich) and phytoplankton biomass (> 18 μg L^{-1} = phytoplankton-rich) identified four lake regimes – 23% of lakes were 'SAV and phytoplankton-poor', 49% were 'SAV-rich' and phytoplankton-poor, 17% were 'phytoplankton-rich' and SAV-poor, and 12% were 'SAV and phytoplankton-rich'.

I explored three lines of evidence to determine if the SAV-rich and SAV-poor lakes exhibited alternative stable states, as recommended by Scheffer and Carpenter (2003). Firstly, I examined whether lake regimes shifted abruptly over time. Most of the lakes were unstable and shifted frequently from year-to-year. Only two of the twenty-three study lakes were stable and remained SAV-rich all seven years, seven lakes switched once, eight lakes switched twice, four lakes switched three times, and two lakes switched four times (Figure 3-2a). There were large differences in the average percentage of lakes that were SAV-rich during the study period – the lowest percentage (43%) occurred in 2002 and 2004 and the maximum percentage (90%) occurred in 2007 (Figure 3-2b). Secondly, I examined the data distribution of SAV cover and phytoplankton biomass for evidence of bimodality. SAV cover exhibited no evidence of bimodality (Figure 3-3a), whereas phytoplankton biomass showed greater frequency above and below 15 – 20 µg chl-*a* L^{-1}, suggesting some support for alternative stable states. Thirdly, I examined the chl-*a* – TP relationships and the turbidity – chl-*a* relationships to test whether the response of the system to key control factors is best described by two separate functions or one single regression. The best chl-*a* – TP model had the same slope but different intercepts for SAV-rich and SAV-poor lakes (Figure 3-4). The covariate model describes this relationship:

Log Chl-*a* = 0.848 Log TP – 0.378 (SAV-poor lakes), - 0.578 (SAV-rich lakes), ($R^2 = 0.39$, , F = 43.84, d.f. = 2, 151, $P < 0.0001$).

The mean chl-*a* concentration of the SAV-poor lakes is significantly higher and almost twice that of the SAV-rich lakes with similar initial TP concentrations, indicating there is approximately double the log chl-*a* in the SAV-poor lakes per unit log TP than in SAV-rich lakes. This indicates that there are different relationships between a key control variable (TP) and a key response variable (chl-a) between alternative regimes, providing support for the existence of alternative stable states.

The turbidity and Chl-*a* relationship was best modelled by one function for all study lakes as follows:

$\text{Log Turbidity} = 0.385 \text{ Log Chl-}a + 0.198$; $R^2 = 0.273$; $F = 48.1$; $P < 0.0001$; d.f. = 1, 128.

This indicates that the turbidity response to chl-a biomass did not differ for SAV-rich and SAV-poor lakes.

SAV-rich regime: abiotic conditions and biotic communities

The limnological conditions of SAV-rich and SAV-poor lakes differed for several key variables (Appendix C). SAV-rich lakes were half as turbid (3.6 NTU versus 6.3 NTU, $P = 0.012$) and had higher water clarity (secchi: max. water depth = 91.3 cm versus 83.8 cm; $P = 0.049$). Total nitrogen concentrations were significantly lower in SAV-rich lakes (2298 versus 3003 μg L^{-1}; $P = 0.012$)., as were TP concentrations (79.4 versus 114 μg L^{-1}; $P = 0.082$), although the results were not significant. Silica concentrations were significantly lower in SAV-rich lakes (1.6 mg L^{-1} versus 2.5 mg L^{-1}). The SAV-rich regime tended to be shallower (102 versus 120 cm), although the difference was not significant.

The primary producer communities differed between SAV-rich and SAV-poor lakes (Table 3-1). SAV-rich lakes had significantly more SAV cover (SAV cover rating = 3.9/5 versus 2.0/ 5, P = <0.0001; SAV cover = 54% versus 21%), P = 0.035) and biomass (mean = 72 g m^{-2} versus 26 g m^{-2}) (Table 3-2). Periphyton biomass was 3X lower in SAV-rich lakes (7218 μg m^{-2} versus 2749 μg m^{-2}; n.s.). The biomass of labile pigments, in particular fucoxanthin, was 9X higher in SAV-poor lakes (2066 μg m^{-2} versus 234 μg m^{-2}; $P = 0.036$). These pigments have been associated with periphytic diatom populations in shallow lakes in boreal Canada (Sokal et al. 2008; McGowan et al. 2011). Violaxanthin was the only periphyton pigment that was higher in SAV-rich lakes, although this was not significant. Phytoplankton biomass was 2X lower in SAV-rich lakes (17.1 µg L^{-1} versus 37.2; P = 0.0002), and phytoplankton cell counts were 14.5X lower (P = 0.001). The phytoplankton community differed between SAV-rich and SAV-poor lakes. SAV-rich lakes had lower densities of the cyanobacteria (68% of phytoplankton community versus 77%, P = 0.009), in particular Chroocales, (26X lower; P = 0.004), Microcystis (23X lower, not significant) and Nostocales (6X lower, n.s.). Other differences were 3X lower Chlorophyta, 2X lower Euglenophyta, 3X lower diatoms, 4X lower Dinophyta. Only Cryptophyta (3X) and Chrysophyta (1.4X) were more abundant in SAV-rich lakes.

Total zooplankton biomass was approximately equal in SAV-rich (407 µg l^{-1}) and SAV-poor lakes (393 µg l^{-1}) (Table 3-1). Cladocerans were significantly more dominant in SAV-rich lakes than SAV-poor lakes (64% versus 50%; P = 0.010). Large Cladocera were less dominant in SAV-rich lakes (59% versus 69% of the Cladocera community, P = 0.062), including *Daphnia* spp. and *Diaphanosoma birgei*, however *Simocephalus vetulus* was significantly more dominant (10% versus 4%; P = 0.002). Chydoridae (principally *Chydorus sphaericus,* and other benthic species) was significantly more dominant (21% versus 10%, P = 0.003), as was *Polyphemus pediculus* (4% versus 1%; P = 0.009). Several cladoceran species associated with SAV, including *Simocephalus vetulus,* and several Chydoridae species including *Graptoleberis testudinaria, Alona guttata, Camptocercus* sp., and *Pleuroxus procurves,* were more prevalent in the

SAV-rich lakes. There were no differences in zooplankton taxa richness between SAV-rich and SAV-poor lakes.

Macroinvertebrate biomass was approximately 2X higher in SAV-rich lakes (Table 3-1) due to higher densities of predators (2X higher, primarily Dyticidae, Odonata, Hemiptera; P = 0.03), scrapers (3X higher, principally snails), gatherers (2X higher, principally *Hyalella azteca*) and filterers (2X higher, Pisidiidae). Only shredders (principally *Gammarus lacustris*) were lower in SAV-rich lakes. Macroinvertebrate taxa richness was approximately twice has high in SAV-rich lakes (19 taxa / sample versus 11 taxa per sample, P = 0.029).

SAV-poor lakes were twice as likely to have fish present (25% of lakes) compared to the SAV-rich lakes (13% of lakes), although the difference was not significant (P = 0.087).

The chlorophyll-*a*: TP ratio of SAV-rich lakes was significantly lower than SAV-poor lakes (0.23 versus 0.35, P = 0.011), indicating approximately 50% less chlorophyll-*a* per unit of TP. The cladocera/ chl-*a* ratio was 2X greater in SAV-rich lakes (53 versus 26; P = 0.0001) , indicating significantly higher zooplankton grazing pressure on phytoplankton (Table 3-1).

Phytoplankton-rich regime: abiotic conditions and biotic communities

Phytoplankton-rich lakes were twice as turbid (8.2 NTU versus 3.4 NTU, P < 0.0001) and less transparent (Secchi depth = 63 cm versus 79 cm, P = 0.0006; Secchi depth: max. depth = 76 versus 93, P < 0.0001) (Table 3-1) compared to phytoplankton-poor lakes. Dissolved organic carbon was twice as high (96.8 mg L^{-1} versus 58.2 mg L^{-1}). The nutrient status was significantly higher in phytoplankton-rich lakes with 2.5X higher TP concentration ($P < 0.0001$), 1.5X higher TN ($P < 0.0001$). The phytoplankton-rich lakes were significantly more N-limited (N:P ratio = 13 versus 19, $P < 0.0001$) and there was less available phosphorus (SRP = 11.2 versus 13.2 $\mu g\ L^{-1}$, $P < 0.015$). Sodium (3.6 versus 2.3 $\mu g\ L^{-1}$, $P < 0.038$) and silica (3.3 versus 1.4 $\mu g\ L^{-1}$, $P < 0.0002$) concentrations were significantly higher compared to phytoplankton-poor lakes (Table 3-1).

Phytoplankton-rich lakes had ten times higher Chl-*a* biomass (72 $\mu g\ L^{-1}$ versus 7 $\mu g\ L^{-1}$, $P < 0.0001$) and 15X higher phytoplankton counts ($P < 0.0001$) compared to phytoplankton-poor lakes (Table 3-1). The phytoplankton-rich lake community was composed of higher densities of Chroocales (14X higher, $P < 0.0001$), Microcystis (23X, n.s.), Nostocales (26X, n.s.), Chlorophyta (4X, $P = 0.0004$), Euglenophyta (3X, n.s.) and Cryptophyta (2X, $P = 0.492$). Edible algae (unicellular algae < 35 μm) was two times higher in phytoplankton-rich lakes ($P = 0.0001$), as was the proportion of the phytoplankton that was cyanobacteria (79% versus 69%; $P = 0.006$).

SAV abundance was lower in phytoplankton-rich lakes, although the differences were only significant based on the SAV cover rating (2.6/5 versus 3.4/5; $P = 0.0004$).

Phytoplankton-rich lakes had approximately twice as much periphyton as phytoplankton-poor lakes, although Chl-*a* was the only pigment with a significant difference ($P = 0.053$).

Total zooplankton biomass was approximately equal in phytoplankton-rich (386 $\mu g\ l^{-1}$) and phytoplankton-poor lakes (408 $\mu g\ l^{-1}$) (Table 3-1). However, there were key differences in the community composition of zooplankton between the lake regimes. In phytoplankton-rich lakes, large cladocerans formed a significantly higher proportion of the Cladocera community (74% versus 58%, P = 0.005), especially *Daphnia* spp. and *Diaphanosoma birgei,* whereas *Simocephalus vetulus* was less abundant. Chydoridae (19% versus 11%, P = 0.015), and *Polyphemus pediculus* (3% versus 1%; P = 0.038) were significantly more dominant in phytoplankton-rich lakes.

Macroinvertebrate biomass, community composition, and biodiversity was similar for phytoplankton-rich and poor lake regimes. There were no differences in fish prevalence.

The chlorophyll-*a*: TP ratio of phytoplankton-rich lakes was 5X higher than phytoplankton-poor lakes (0.63 versus 0.14, P < 0.0001), indicating higher chlorophyll-*a* per unit of TP. The cladoceran: chl-*a* ratio was 11X lower in phytoplankton-rich lakes (56 versus 5; P < 0.0001), indicating significantly lower zooplankton grazing pressure on phytoplankton (Table 3-1).

Factors affecting the persistence of alternative regimes

Boreal Plains lakes were persistent in the SAV-rich (> 25% SAV cover) 61% of the study period (Figure 3-5a), whereas the lakes were persistent in the phytoplankton-rich only 30% of the time (Figure 3-5b).

Overall, the persistence of the SAV-rich regime and phytoplankton-rich regimes were best predicted by lake-specific variables. The persistence of the SAV-rich regime was best predicted by maximum water depth, macroinvertebrate predator biomass and TP (variance explained = 66%) (Figure 3-6). The SAV-rich regime was least persistent (35% of years SAV-rich) in deeper lakes (> 111.5 cm max. depth), whereas the regime was more persistent (67% of years SAV-rich) in shallower lakes (<111.5 cm max. depth). Shallow lakes were further partitioned based on abundance of macroinvertebrate predators. Lakes with high biomass of predaceous macroinvertebrates exhibited the most persistent SAV-rich regime (83% of years). Finally, the SAV-rich regime was more persistent (71% of years) in mesotrophic lakes (TP < 57.5 $\mu g\ L^{-1}$), versus more eutrophic lakes that were SAV-rich 51% of the time.

Landscape variables that best predicted the persistence of the SAV-rich regime included the extent of wetland in the local buffer area, lake elevation and lake area (variance explained = 59%) (Figure 3-7). The SAV-rich regime was least persistent (36% of years) in lakes with a higher proportion of wetland in the buffer area (> 65%). Lakes with less wetland in the buffer area were further partitioned by lake elevation. Lakes low in the regional flow path (< 659 m) exhibited the highest persistence in the SAV-rich regime (80% of years). Finally, lake area was a tertiary predictor of the persistence of SAV-rich regime. Smaller lakes (<6.7 ha) tended to exhibit a more persistent SAV-rich regime (67% of years) compared to larger lakes (40% of years).

The persistence of the phytoplankton-dominated regime was best predicted by *Daphnia* dominance and TP (variance explained = 50%) (Figure 3-8). The phytoplankton-rich regime was more persistent (57% of years) in lakes with a high dominance of *Daphnia* (> 61% of the cladoceran community). Lakes with low dominance of *Daphnia* were further partitioned based on TP status. The phytoplankton-rich regime was more persistent (31% of years) in eutrophic lakes (TP > 67 μg L^{-1}) compared to mesotrophic lakes (13% of years).

Landscape variables that best predicted the persistence of the phytoplankton-rich regime included lake area and Ca + Mg (total variance explained = 23%) (Figure 3-9). The most persistent phytoplankton-rich regime (41% of years) was observed in smaller lakes (< 5.2 ha). Larger lakes were further partitioned based on the concentration of calcium and magnesium. Lakes with higher Ca + Mg (> 37.7 mg L^{-1}) exhibited a more persistent phytoplankton-rich regime (36% of years) compared to lakes with less Ca + Mg (17% of years).

Discussion

Alternative regimes in shallow lakes on the Boreal Plains

Our study lakes differ from the initial model proposed by Scheffer et al. (1993). I identified four lake regimes using previously established threshold values of SAV cover (> 25% cover = SAV-rich) and phytoplankton biomass (> 18 μg L^{-1} = phytoplankton-rich) – 23% of lakes were SAV and phytoplankton-poor, 49% were SAV-rich and phytoplankton-poor, 17% were phytoplankton-rich and SAV-poor, and 12% were SAV and phytoplankton-rich. These four lake regimes were observed previously in a broader synoptic survey in the region (Bayley et al. 2003).

I explored whether SAV-rich versus SAV-poor regimes showed evidence of an alternative stable state response to changing environmental conditions following analyses recommended by Scheffer and others (2003). There was some evidence of an alternative *stable* state response – the two lake regimes had significantly different TP – Chl-*a* relationships, and there were significant differences in the abiotic conditions and biotic communities that suggest a suite of positive feedback mechanisms are maintaining the regimes. However, a greater number of other observations indicated a lack of support for alternative stable states including: 1) many of the lakes switched states from year to year; 2) there was no bimodality in the distribution of SAV cover and phytoplankton biomass; 3) the turbidity – chl-*a* and turbidity – SAV cover relationships were similar for both regimes.

Overall, a threshold of > 25% cover of SAV appears to coincide with alternative regimes that affect key differences in the limnological conditions and biological communities of shallow lakes on the Boreal Plains. I was unable to determine from field data alone if this is simply a threshold response or if the response pattern is consistent with alternative stable state theory. Additional evidence from experimental tests or theoretical models is needed to better understand the relationship between the alternative regimes and changing environmental variables (Scheffer et al. 2003).

Within lake processes affecting the resilience of the SAV-rich regime

The SAV-rich regime appears to be maintained through a combination of bottom-up and top-down mechanisms within the lake. SAV dominance is associated with lower turbidity and increased water clarity in shallow lakes on the Boreal Plains. Turbidity levels and Secchi depths were lower in SAV-rich lakes. The structure of SAV acts to baffle currents, and the roots help to stabilize the sediments (Jeppesen et al. 1997). Dense SAV beds trap twice as much bulk sediment per unit area compared to open water areas of lakes (Rooney et al. 2003). However, the turbidity – chl-*a* relationship was weak ($R^2 = 0.27$) and there were no significant differences in the relationship between SAV-rich and SAV-poor lakes. This suggests that factors other than phytoplankton biomass strongly affect turbidity in these lakes. The lower turbidity levels in SAV-rich lakes is likely due to reduced sediment re-suspension.

Another mechanism helping to maintain the SAV-rich regime in shallow lakes is competition between phytoplankton and other algae such as epiphyton for nutrients (Scheffer et al. 1993; Barko et al. 1998). Natural systems uptake nitrogen and phosphorus and recycle them as tight commodities (Moss 2008). Nutrient levels, in particular TN and silica, were significantly lower in SAV-rich lakes. Nutrient assimilation by SAV may result in lower nutrients in the water column. Another potential mechanism is reduced re-suspension of nutrient-rich sediments in SAV-rich lakes. The role of nitrogen limitation on phytoplankton biomass is uncertain because at low inorganic N, when the TN: TP ratio declines below 10, it may trigger a switch in the community to nitrogen-fixing cyanobacteria (Smith 1983). The Chl-*a* – TP relationship differed between SAV-rich and SAV-poor lakes, consistent with Scheffer and other's (1993) conceptual model. In SAV-poor lakes the chl-*a* biomass was higher per unit of TP, likely due to higher concentrations of cyanobacteria. This pattern is consistent with shallow lakes in the prairie region of southern Alberta (Jackson 2003).

There appears to be strong top-down control of phytoplankton in SAV-rich lakes. The ratio of cladocerans/ chl-*a*, which is used as an index of microcrustacean herbivory on phytoplankton (Mazumder et al. 1990; Jeppesen et al. 2004), was two times higher in SAV-rich lakes than SAV-poor lakes. Additionally, 64% of the zooplankton community was composed of cladocerans that graze on phytoplankton in SAV-rich lakes compared to 50% in SAV-poor lakes. Several cladoceran species associated with SAV were more prevalent in the SAV-rich lakes. *Simocephalus vetulus* is a large plant-associated filter-feeder that likely obtains a large proportion of its diet from periphyton material (Dodson et al. 2001). They also graze phytoplankton and appear to contribute to increasing water transparency in the water column of vegetation-dominated shallow lakes (Dodson et al. 2001). *S. vetulus* is often associated with macrophytes because they are weak swimmers (Balayla et al. 2004). The high proportion of cladocerans is typical of lakes with low fish predation pressure on zooplankton (Jeppesen et al. 2000; Zimmer et al. 2002). Cladoceran dominance of the zooplankton community was high compared to lakes in southern Alberta and Denmark (both 47%) (Jackson et al. 2007). Fish presence was two times lower in SAV-rich lakes compared to SAV-poor lakes. This suggests that the presence of brook stickleback, via consumption of large zooplankton grazers, promotes phytoplankton biomass in these lakes. This supports earlier findings in shallow lakes on the Boreal Plains (Norlin et al. 2005), and other shallow lake systems (Jeppesen et al. 1990; Hanson et al. 1994; Zimmer et al. 2001).

There also appears to be an important benthic pathway promoting SAV-dominance in these lakes. SAV-rich regimes were associated with higher abundance of macroinvertebrates including predators (2X) and gastropods (3X), which corresponded with lower periphyton biomass. Grazing macroinvertebrates likely suppress epiphyton that would otherwise shade SAV. Macroinvertebrate grazers can play an important role in maintaining the high macrophyte biomass in clear water lakes via suppression of periphyton (Jones et al. 2003). Laboratory studies show that the presence of freshwater snails can increase SAV growth and leaf longevity due to nutrient removal and removal of epiphyton (Bronmark 1985; Underwood 1991; Underwood et al. 1992). Field evidence suggests that periphyton biomass is primarily constrained by grazers rather than nutrients (Jones et al. 2002; Jones et al. 2003; McIntyre et al. 2006) and Hillebrand (2002) for a review.

SAV-rich lakes were associated with a higher taxa richness of macroinvertebrate species. In terrestrial systems, higher species richness has been shown to have important implications for community stability (Tilman 1999). Higher taxa richness may increase the resilience of the SAV-rich regime in the face of disturbance, such that the loss of one taxa may result in another taxa filling the vacant ecological niche. Variability in responses of species within functional groups to environmental change is critical to ecosystem resilience (Chapin et al. 1997; Norberg et al. 2001). In shallow lakes, the loss of SAV species richness has been hypothesized to result in reduced resilience of the SAV-rich regime and a loss of SAV dominance (Sayer et al. 2010).

Within lake processes affecting the resilience of the phytoplankton-rich regime

Phytoplankton-rich lakes were shallower, more turbid, and had higher concentrations of nutrients, DOC, silica and Na^+ compared to phytoplankton-poor lakes. Similar limnological signatures have been observed in very shallow (< 50 cm depth), closed basins in the Peace-Athabasca floodplain that are highly influenced by precipitation inputs and evaporative processes (Wolfe et al. 2007). These conditions suggest that the phytoplankton-rich lakes are subject to the evaporative concentration of nutrients and remobilization of ions following rain events leading to higher turbidity and higher phytoplankton biomass. This is an important mechanism influencing phytoplankton production in other boreal (Schindler et al. 1996) and deltaic (Sokal et al. 2008; Loverde-Oliveira et al. 2009; McGowan et al. 2011) systems.

Phytoplankton-rich lakes were more dominated by cyanobacteria (79% compared to 69% in phytoplankton-poor lakes), particularly Chroocales and Nostacales, and Chlorophyta (4X higher compared to phytoplankton-poor lakes). The phytoplankton-rich lakes were less P-limited (TN:TP ratio = 13 versus 19 in phytoplankton-poor lakes), which may favour cyanobacteria dominance. Eutrophic shallow lakes and ponds are often dominated by cyanobacteria (Schindler 1977; Smith 1983; Reynolds 1984) and chlorophytes (DeNoyelles et al. 1978; Jeppesen et al. 1990; Jensen et al. 1994). The dominance of heterocystous cyanobacteria, non-heterocystous cyanobacteria and chlorophytes has been observed to vary along a gradient of phosphorus availability (Jensen et al. 1994). Non-heterocystous cyanobacteria favoured intermediate TP concentrations and heterocystous cyanobacteria favoured low TP concentrations (Jensen et al. 1994). I observed primarily non-heterocystous cyanobacteria (D. Cobbaert, personal observation), suggesting TP concentrations were in the intermediate portion of the gradient.

There was evidence that food web effects on phytoplankton are weak in phytoplankton-rich lakes: edible algae were abundant (unicellular < 35 μm), the chlorophyll-*a* per unit TP was significantly higher, and the cladoceran/ chl-*a* ratios were significantly lower, which is used as an index of microcrustacean herbivory on phytoplankton (Mazumder et al. 1990; Jeppesen et al. 2004). Phytoplankton-rich lakes had a lower proportion of cladocerans (52% versus 69%) and a higher proportion of calanoids (29% versus 16%) and cyclopoids (14% versus 9%). This pattern of zooplankton community structure has been documented in other turbid lakes (Reinertsen et al. 1990; Cottenie et al. 2001).

I had hypothesized that phytoplankton-rich lakes would be associated with a greater prevalence of planktivorous fish, similar to other shallow lake studies (e.g. Christoffersen et al. 1993; Vanni et al. 1997; Zimmer et al. 2001). Fish predation is often emphasized as a primary regulator of zooplankton populations, and can significantly alter the size structure and composition of zooplankton communities, which in turn can promote phytoplankton biomass (Brooks et al. 1965; Carpenter et al. 1993; Mazumder 1994). However, based on the small sample size in this study (only 5 of 23 lakes were fish-bearing) the prevalence of brook stickleback was similar in phytoplankton-rich and phytoplankton-poor lakes. This suggests that brook stickleback are not a dominant factor contributing to high phytoplankton biomass in these lakes. The top-down effects of brook stickleback may be weak in these lakes. They have a small gape size and tend to target cladocerans and small chironomids (Tompkins et al. 1983), and densities in central Alberta (McParland et al. 2006) were much lower than shallow lakes in New York (Batzer et al. 2000) and Minnesota (Zimmer et al. 2001). Top-down effects of small planktivorous fish on phytoplankton appear relatively weak, which is consistent with studies of North American prairie lakes (Zimmer et al. 2001; Jackson 2003; Jackson et al. 2007).

A small but notable body of research has focused on zooplankton communities in shallow, fishless ponds (Lynch 1978; Smith et al. 1982; Steiner 2003; Steiner et al. 2003). These studies suggest that zooplankton community structure may be determined by a variety of factors including top-down control by predators, abiotic conditions that affect physiologically-based tolerances, and/ or bottom-up resource based effects.

Top-down control by macroinvertebrate predators (e.g. Dytiscids, *Chaoborus*, and Notonectids) may affect the size structure and grazing capacity of zooplankton in fishless lakes (e.g. Murdoch et al. 1984; Mackay et al. 1990; Vanni et al. 1990; Arner et al. 1998; Shurin 2000; Cobbaert et al. 2010). However, there were no differences in macroinvertebrate predators between phytoplankton-rich and phytoplankton-poor lakes suggesting that this is not a dominant mechanism contributing to zooplankton community structure in these lakes.

Phytoplankton abundance may be an important influence on zooplankton competitive outcomes. Large cladocerans, including *Daphnia*, may be favoured at high levels of resource abundance, whereas small-bodied taxa may dominate at low resource levels (Romanovsky et al. 1985). Large cladocerans constituted a larger proportion of the Cladocera population in phytoplankton-rich lakes (74%) compared to phytoplankton-poor lakes (58%). The greater dominance of large cladocerans in the phytoplankton-rich lakes is consistent with the higher abundance hypothesis, as these lakes had a higher abundance of total phytoplankton, including edible algae (< 35 μm). Nutrient stoichiometry (i.e. C:N:P content) of algae is another important aspect of resource quality. *Daphnia* generally have higher phosphorus requirements compared to *Simocephalus vetulus* and many small-bodied Cladocera and copepods, and may be favoured when algal C:P and N:P ratios are low (Sterner et al. 1994; Urabe et al. 1997; DeMott 1998; Steiner et al. 2003). The lower biomass of *Simocephalus vetulus* and Chyoridae in phytoplankton-rich lakes, which are more P-limited, is consistent with the mineral-limitation hypothesis.

Lake factors predicting persistence of the SAV-rich regime

The persistence of the SAV-rich regime was best predicted by maximum lake depth, predaceous macroinvertebrate biomass and TP. Deeper lakes (> 112 cm) tended to support the least persistent SAV-rich regime. Deeper lakes may limit SAV growth due to light limitation and negative trophic effects from fish. A SAV biomass – lake depth survey in the region found a unimodal relationship with SAV biomass peaking at 125 cm water depth (Chapter 4). SAV growth is presumably limited at shallower depths (< 125 cm) by increased turbidity, and at deeper depths (> 125cm) by light attenuation due to increasing water depth. There was little SAV biomass beyond 175 cm depth. Another factor associated with deeper lakes is an increased prevalence of planktivorous fish. Maximum lake depth was significantly higher in fish-bearing lakes compared to fishless lakes (153 cm versus 101 cm, $P < 0.0001$). Fish presence was two times lower in SAV-rich lakes compared to SAV-poor lakes. This suggests that fish, via top-down predatory effects on large zooplankton grazers, promote a turbid water state in these lakes, as previously observed in shallow lakes on the Boreal Plains (Norlin et al. 2005), and other shallow lake systems (Jeppesen et al. 1990; Hanson et al. 1994; Zimmer et al. 2001).

The positive association between biomass of predaceous macroinvertebrates and the persistence of the SAV-rich regime suggests that predaceous macroinvertebrates may play an important role in stabilizing the regime. The macroinvertebrate community was largely ignored in the initial model of Scheffer et al. (1993), likely because fish are common in European and temperate North American lakes where the model was developed. Large predatory macroinvertebrates are top predators in shallow fishless lakes where they are abundant and diverse compared to fish-bearing water bodies (Mallory et al. 1994; Batzer et al. 1996; Wellborn et al. 1996; Tonn et al. 2004; Hornung et al. 2006). Mesocosm experiments in the study lakes found *Dytiscus alaskanus,* a predaceous macroinvertebrate, capable of precipitating a trophic cascade via algivorous snails and other herbivores leading to increased production of periphyton (Cobbaert et al. 2010). Other studies have also found predatory macroinvertebrates, including dragonfly larvae and *Notonecta,* capable of precipitating a trophic cascade effect on periphyton (Blaustein et al. 1995; Stav et al. 2000).

Lower TP concentration ($< 58\ \mu g\ L^{-1}$) was associated with a more persistent SAV-rich regime. Nutrient-loading is known to promote phytoplankton biomass, increase turbidity and suppress SAV coverage (Jeppesen et al. 1998; Scheffer 1998). Phosphorus is the main limiting nutrient in these lakes, and previous studies have found that switches to a turbid water regime were related to increased TP concentration (Bayley et al. 2007).

Lake factors predicting the persistence of the phytoplankton-rich regime

The persistence of the phytoplankton-rich regime was best predicted by the dominance of *Daphnia* in the Cladocera community and mean TP concentration. High TP was associated with a more persistent phytoplankton-rich regime, as has been previously demonstrated in shallow lakes on the Boreal Plains (Bayley et al. 2007) and numerous other studies of shallow lakes.

I suspect that the association between higher dominance of *Daphnia* is driven by bottom-up processes rather than top-down trophic effects. None of the highly persistent phytoplankton-rich lakes with high *Daphnia* dominance were fish-bearing. Higher *Daphnia* dominance has been associated with higher levels of resource abundance (Romanovsky et al. 1985), as well as their ability to access a broader size spectrum and large size classes of algae compared to many small-bodied zooplankton (Burns 1968; Neill 1975; DeMott 1995). *Daphnia* have higher phosphorus requirements compared to *Simocephalus vetulus* and many small-bodied Cladocera and copepods, and may be favoured when algal C:P and N:P ratios are low (Sterner et al. 1994; Urabe et al. 1997; DeMott 1998; Steiner et al. 2003).

Landscape factors predicting the persistence of alternative regimes

Lake elevation

Lakes lower in elevation tended to support a more persistent SAV-rich regime. The effects of drought are likely attenuated in lowland lakes due to increased hydrologic inputs from upstream sources, such as shallow groundwater pathways from local peatlands (Ferone et al. 2004). Shallow lakes on the Boreal Plains have been observed to exhibit variations in TP responses to logging along a elevation gradient (Devito et al. 2000). Recharge lakes, located higher in the flow system, showed higher TP responses to logging activity in their catchments compared to lower elevation flow-through lakes (Devito et al. 2000). Likewise, spatial patterning in dynamics was observed in response to drought in a groundwater-dominated system in northern Wisconsin. During drought, as local flow paths reverse or diminish, groundwater from more stable regional flow paths is thought to provide a larger proportion of the water input to lowland lakes (Webster et al. 2000).

Wetland extent in buffer

Contrary to my hypothesis, increased wetland area in the local catchment decreased the persistence of the SAV-rich regime. It is likely that the wetlands are functioning primarily as a source of phosphorus to lakes, which is eclipsing their role as an attenuator of droughts. Wetland extent in a lake's catchment has been correlated with increased lake TP in shallow lakes on the Boreal Plains (Devito et al. 2000). A process-based hydrology study found surface hydrologic connections to wetlands were the dominant source of phosphorus to the annual P budget of two shallow lakes on the Boreal Plains (Ferone 2001). In contrast, in regions with high agriculture and urban land use, wetland extent in a catchment has been associated with decreased TP concentrations (Detenbeck et al. 1993; Weller et al. 1996; Diebel et al. 2009; Fergus et al. 2011). Wetlands in disturbed areas may function as nutrient sinks by intercepting phosphorus runoff from agriculture and urban activities that would otherwise flow into surface water bodies (Moustafa 1999).

Lake area

Smaller lakes promoted the persistence of both phytoplankton-rich and SAV-rich regimes, although I propose that lake size affected the persistence of the primary producer communities differently. Smaller lakes likely promoted the phytoplankton-rich regime through increased susceptibility to evaporative concentration during drought, which has been associated with increased phytoplankton biomass in shallow lakes on the Boreal Plains (Chapter 4). Evaporative concentration of nutrients and organic matter in isolated lakes is an important mechanism influencing phytoplankton production, as seen in other boreal lakes (Schindler et al. 1996), in Lake Vortsjarv, a large shallow lake in Estonia (Noges et al. 1999) and several floodplain lakes (Sokal et al. 2008; Loverde-Oliveira et al. 2009; McGowan et al. 2011).

The persistence of the SAV-rich regime was likely higher in smaller lakes due a variety of mechanisms. Although the mechanisms cannot be resolved here, the positive effect of lake size on the stability of a SAV-dominated state in these lakes may be associated with wind effects, colonization time, nitrogen retention time and fish effects. Other studies have similarly found that smaller lakes tend to remain in a vegetated state longer and may tend to be systematically closer to a vegetated stable state (Jeppesen et al. 1990; Van Geest et al. 2003; Sondergaard et al. 2005; Scheffer et al. 2006; Van Geest et al. 2007).

Wind effects are considered a plausible mechanism hindering SAV dominance and persistence in large lakes. Waves and currents have the capacity to disturb, damage and hamper the growth and establishment of SAV in shallow lakes (Hudon et al. 2000; Havens et al. 2004). An aquatic plant in moving water experiences 25X more force in the same wind velocity as a terrestrial plant (Denny et al. 2002). The ability of wind to induce waves and currents depends on water depth and the fetch (continuous length of open water in a particular direction) and is therefore influenced by the size, shape and orientation of the lake (Keddy 1982; Hamilton et al. 1997). Hakanson (1982) formulated a “dynamic ratio” to assess wind effects on lakes (calculated as the square root of surface area divided by mean depth). There was a strong relationship between lake area and the dynamic ratio in the study lakes ($R^2 = 0.69$) indicating that larger lakes are more susceptible to the effects of wind, resulting in more physical stress on aquatic plants. However, in very large (> 4.2 km2) eutrophic (60 – 230 $\mu g\ L^{-1}$) lakes in southern Sweden, Weisner et al. (1997) found the opposite pattern. SAV growth was significantly higher at exposed sites compared to sheltered sites. The exposed sites had 5X lower periphyton production thus the wind and currents were postulated to remove periphyton and promote SAV growth (Weisner et al. 1997). This is considered an unlikely mechanism affecting SAV growth in shallow lakes on the Boreal Plains as SAV-rich regimes tended to occur in small lakes that are less affected by wind.

Additionally, colonization of SAV may take several years to complete in large lakes when vegetation is in a sensitive phase (Scheffer et al. 1993). Turbid 'hot-spots' were observed in larger lakes during the study, where a lake was predominately SAV-rich but portions of the lake were turbid, increasing the chance for a switch to a SAV-poor state.

Lake size may affect nitrogen cycling with consequences for SAV abundance and species richness. Higher nitrate concentrations have been observed in lakes > 10 ha likely reflecting higher hydraulic loading (Sondergaard et al. 2005). Nitrogen in small lakes with low hydraulic flushing will eventually be removed from the system with denitrification. Recent studies in shallow lakes indicate that nitrogen (N) may play a significant role for the abundance and species richness of SAV (Gonzalez Sagrario et al. 2005; James et al. 2005). Thus SAV in small lakes may benefit from low nitrogen concentrations.

Fish effects alone are insufficient to explain lake size effects on the stability of the SAV-rich regime, but they may be a contributing factor. Fish presence followed a lake size gradient in the study lakes – there were no fish in lakes < 4.5 ha, intermittent fish presence in lakes 4.5 – 9.5 ha, and permanent fish presence in lakes > 15.5 ha. Fish kills are more common in smaller lakes due to a higher risk of oxygen depletion (Jeppesen et al. 1990). Fish, via top-down predatory effects, promote a turbid water state in these lakes (Norlin et al. 2005), and other shallow lake systems (Jeppesen et al. 1990; Hanson et al. 1994; Zimmer et al. 2001).

Groundwater connectivity

Lakes with higher Ca + Mg tended to support a more persistent phytoplankton-rich regime. This was contrary to my prediction that increased groundwater connectivity would decrease the sensitivity of a lake to fluctuations in precipitation and hence decrease the persistence of the phytoplankton-rich regime. Lakes with higher Ca + Mg tended to occur on organic deposits located lower in the regional district, and tended to have a high proportion of wetland in the local catchment (Appendix E). Lakes with higher Ca + Mg showed less inter-annual variability in phosphorus levels in different lakes on the Boreal Plains (Devito et al. 2000). This suggests that the more persistent phytoplankton-rich regime may be maintained by groundwater flow paths that minimize changes in phosphorus.

Conclusions

Internal positive feedback mechanisms appear important in maintaining the resilience of the SAV-rich regime in fishless lakes on the Boreal Plains. The SAV-rich regime is reinforced (stabilized) by top-down control of phytoplankton and periphyton by macroinvertebrates and zooplankton. However, top-down processes appear weak or absent in the phytoplankton-rich regime, which may contribute to their low persistence.

The most important controls of the persistence of the SAV-rich and phytoplankton-rich regimes were lake-specific features and within lake processes. The SAV-rich regime persistence increased in shallower lakes, with abundant predaceous macroinvertebrate predators, and low TP concentration. Higher persistence of the phytoplankton-rich regime was associated with higher *Daphnia* dominance, and higher TP concentration. However, landscape features may also explain some of the variation in the persistence of alternative regimes. Smaller, lowland lakes, with a higher proportion of wetlands in the local catchment tended to support a more persistence SAV-rich regime. The persistence of the phytoplankton-rich regime may be partially explained by lake size and lake connectivity with groundwater (Figure 3-10).

Tables

Table 3-1. Mean values for physical, chemical and biological parameters in clear and turbid lakes from surveys in August 2001-2007. Each lake in each year was classified as clear or turbid using cluster analysis. Means of all lakes for all years that were classified as clear or turbid are presented. p values are from t-tests or Mann-Whitney U tests as appropriate. * indicates statistical significance at $\alpha = 0.05$, ** indicates statistical significance after a Bonferroni adjustment of $\alpha = 0.05/72 = 0.0007$.

	Units	n	SAV-rich	SAV-poor	P value	Sign.	Phytoplankton-rich	Phytoplankton-poor	P value	Sign.
Primary producers										
SAV abundance	Rating	156	3.9 ± 0.7	2.0 ± 0.6	<0.0001	**	2.6 ± 1.2	3.4 ± 1.0	0.0004	**
Chl-a	µg l^{-1}	156	17 ± 42	37 ± 79	0.0002	**	72 ± 99	7 ± 4	<0.0001	**
Phytoplankton counts	#/ µl	117	26,377 ± 63,529	382,552 ± 987,599	0.001	*	484,455 ± 1,115,668	32,673 ± 95,905	<0.0001	**
Chroocales	#/ µl	117	7,650 ± 35,107	199,048 ± 740,976	0.004	*	240,582 ± 844,097	17,151 ± 84,722	<0.0001	**
Chlorophyta	#/ µl	117	3,695 ± 10,785	11,095 ± 28,285	0.232		13,777 ± 31,920	3,564 ± 10,334	0.000	**
Unicellular algae < 35 µm	#/ µl	117	5,772 ± 34,172	6,184 ± 16,201	0.095		8,265 ± 18,258	4,871 ± 31,533	0.000	**
% Cyanobacteria	%	117	68 ± 27	77 ± 29	0.009	*	79 ± 27	69 ± 29	0.006	*
Periphyton biomass (total)	µg m^{-7}	23	2,669 ± 2,748	7,218 ± 8,020	0.390		4,924 ± 4,342	2,982 ± 4,743	0.504	
Periphyton biomass (Chl-*a*)	µg m^{-2}	23	1,686 ± 1,861	4,083 ± 5,103	0.537		3,161 ± 2,609	1,698 ± 3,008	0.310	
Periphyton biomass (Fucoxanthin)	µg m^{-3}	23	221 ± 465	2,066 ± 2,444	0.030	*	617 ± 1,055	625 ± 1,538	0.972	
Zooplankton										
Total zooplankton	µg L^{-1}	130	407 ± 434	393 ± 565	0.267		386 ± 367	408 ± 539	0.441	
Cladocerans	% total	130	64 ± 23	50 ± 29	0.010	*	51 ± 29	61 ± 25	0.068	~
Calanoida	% total	130	25 ± 10	34 ± 13	0.073	~	33 ± 16	28 ± 9	0.241	
Cyclopoida	% total	130	11 ± 25	11 ± 28	0.436		14 ± 28	9 ± 26	0.194	
Large Cladocerans	% clad.	130	59 ± 26	69 ± 14	0.062	~	74 ± 18	58 ± 24	0.005	**
Zooplankton richness	#/L	65	4.7 ± 4.3	5.1 ± 7.9	0.801		4.6 ± 4.3	4.9 ± 6.6	0.838	
Macroinvertebrates										
Total macroinvertebrates	µg l^{-1}	63	3,730 ± 3,519	2,189 ± 2,428	0.074		3,240 ± 3,391	3,169 ± 3,217	0.968	
Predators	µg l^{-1}	63	964 ± 1,333	409 ± 444	0.026	*	768 ± 1,149	771 ± 1,139	0.692	
Scrapers	µg l^{-1}	63	1,034 ± 1,982	352 ± 409	0.187		789 ± 1,791	799 ± 1,592	0.658	

Macroinvertebrate richness	#/ sample	23	19 ± 6	11 ± 6	0.029	*	18 ± 7	17 ± 7	0.915	
Fish		156	13 ± 0.3	25 ± 0	0.087	~	14 ± 0.3	19 ± 0	0.600	
Trophic indices										
Chl-a: TP	ratio	130	0.23 ± 0.35	0.35 ± 0.58	0.011	*	0.63 ± 0.75	0.14 ± 0.10	< 0.0001	**
Cladoceran: Chl-a	ratio	130	53 ± 77	26 ± 66	0.0002	**	5 ± 9	56 ± 82	< 0.0001	**

Figures

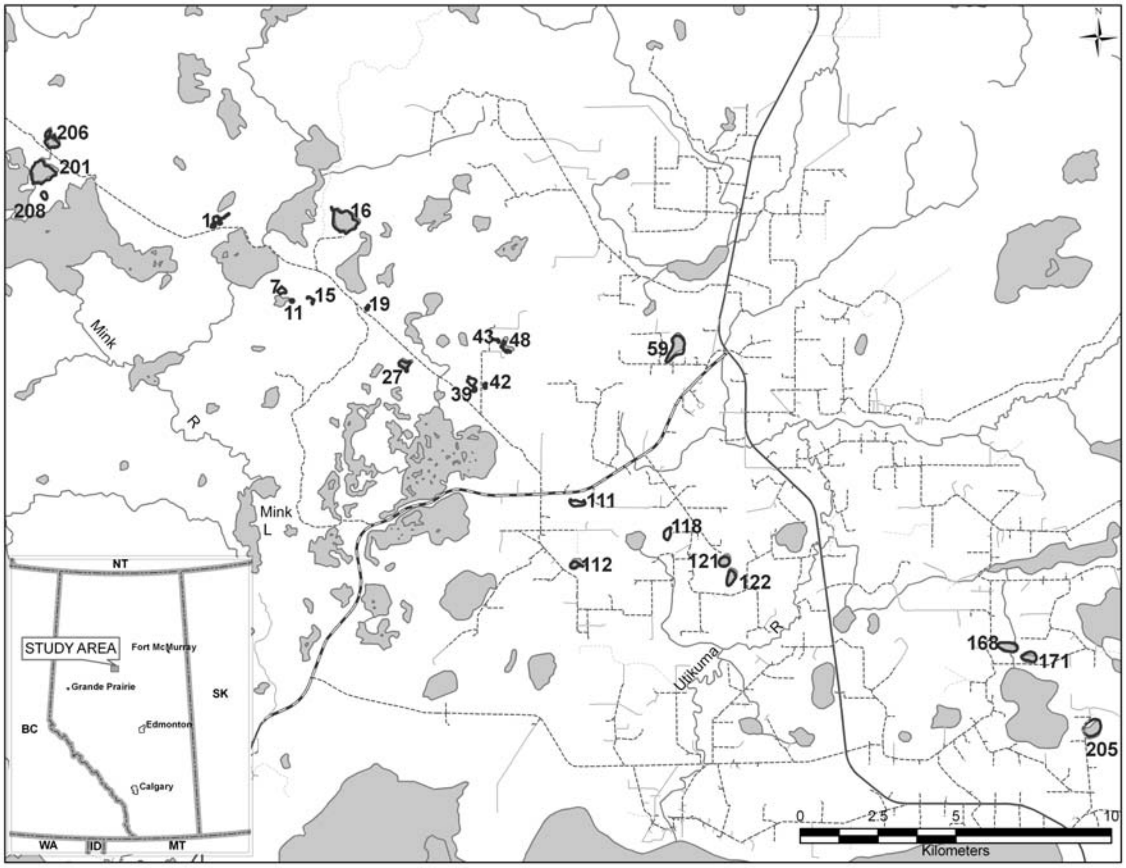

Figure 3-1. Study region showing the location of the 23 study lakes.

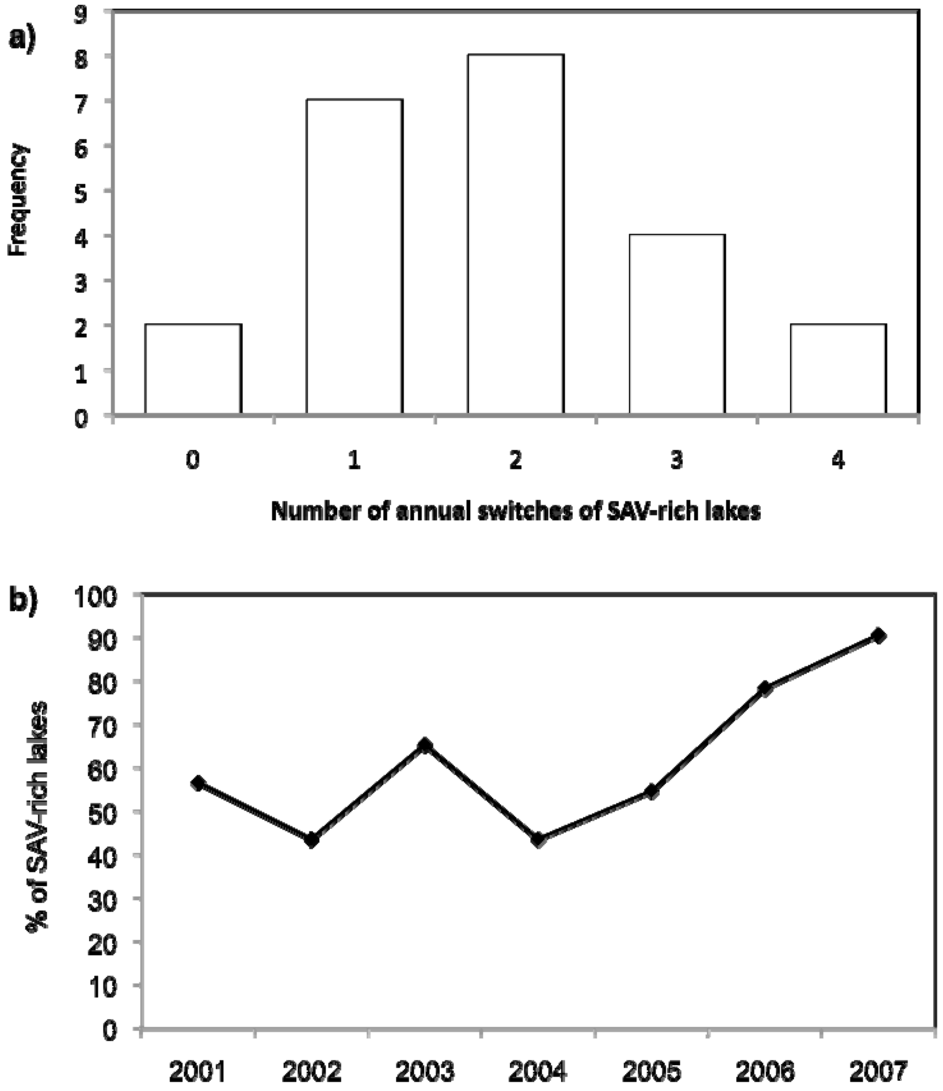

Figure 3-2. a) The number of annual switches of SAV-rich lakes during the seven year study period. b) The average % of lakes that were SAV-rich for each year of the study (n = 23 lakes).

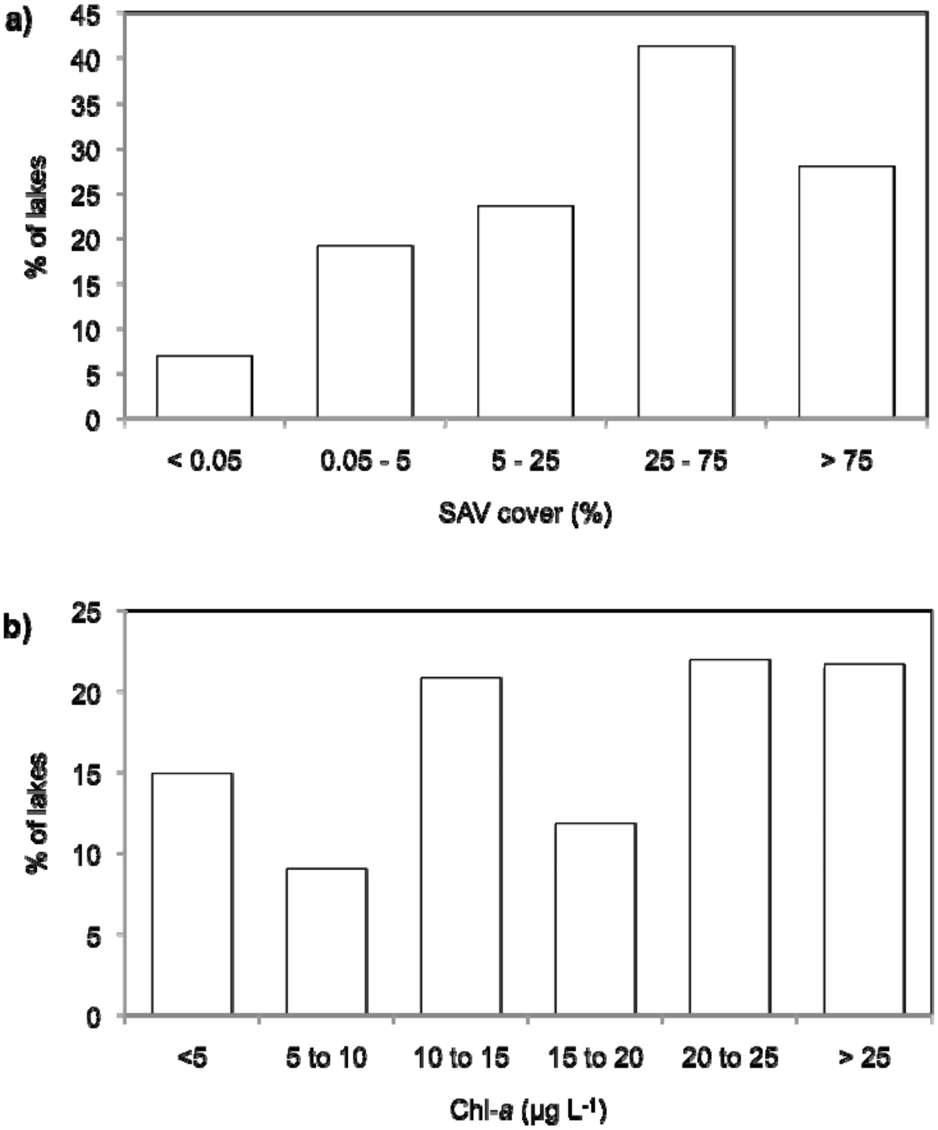

Figure 3-3. Frequency distribution of a) SAV cover and b) chl-*a* in 23 lakes during 2001 to 2007. There is little evidence of a bimodal distribution in either variable.

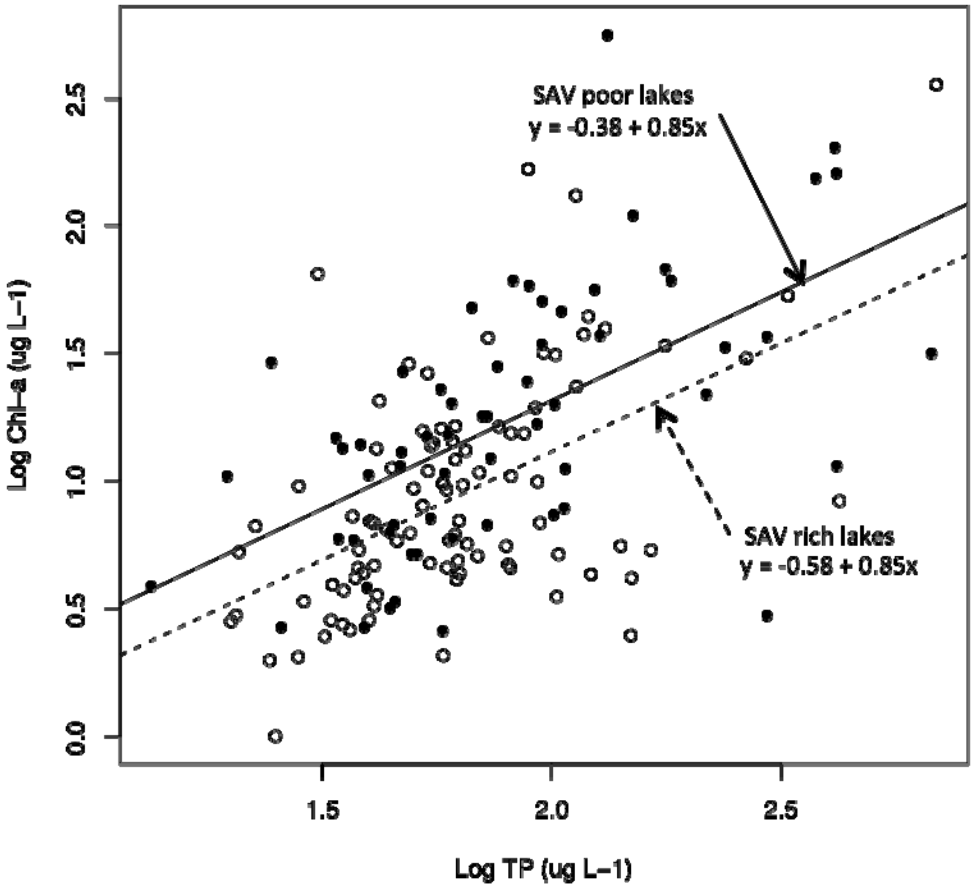

Figure 3-4. Relationship between phytoplankton biomass (chl-*a*) and TP in SAV-poor (solid line, open circles) and SAV-rich (dashed line, solid circles) lakes. ANCOVA analysis and log likelihood ratio tests indicated that the most parsimonious models consisted of the same slope but separate intercepts for the SAV-rich and SAV-poor lakes (R^2 = 0.37, F = 43.84, d.f. = 2,151, P < 0.0001).

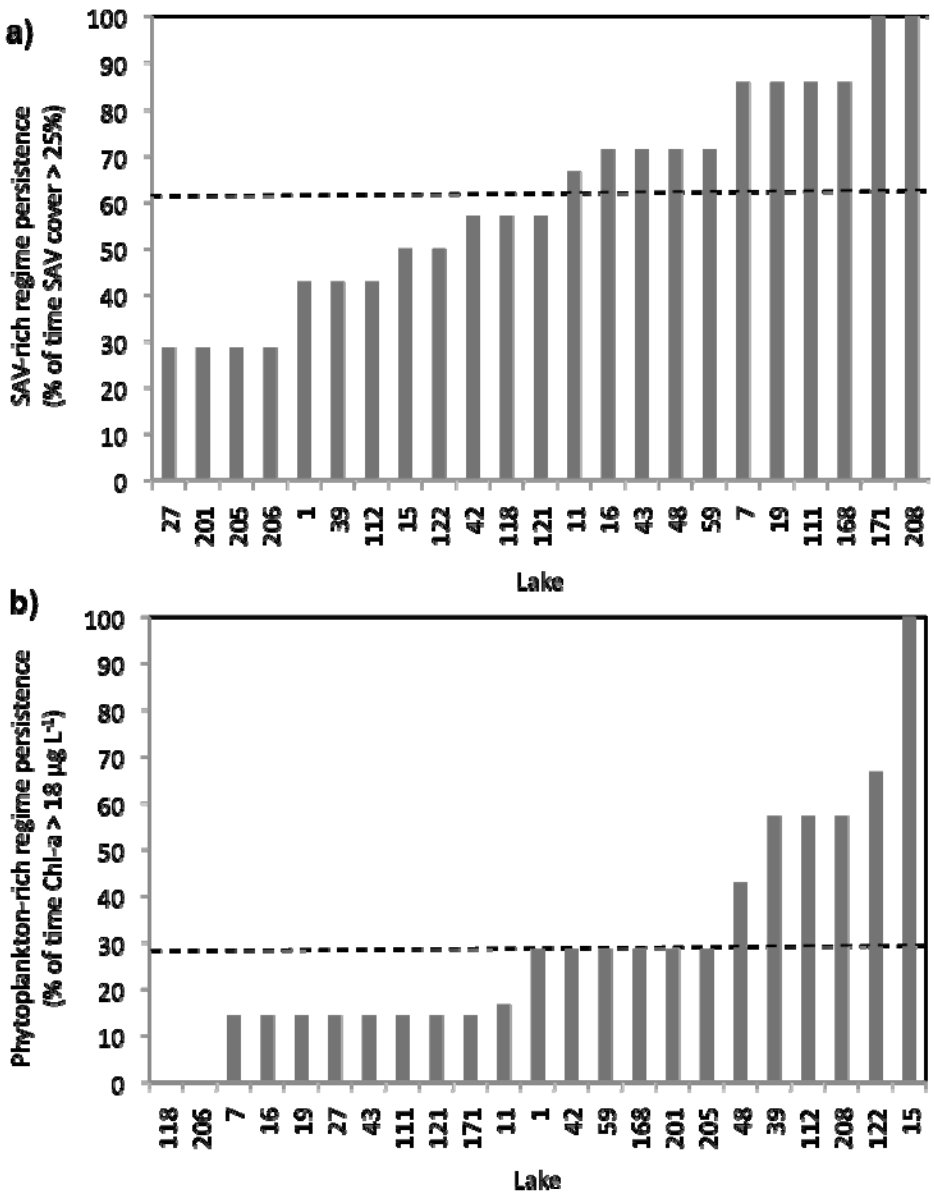

Figure 3-5. Persistence (percentage of years in alternative regimes) of the a) SAV-rich regime and b) phytoplankton-rich regime for each lake during the study period. Dotted lines represent average persistence of all lakes during the study period.

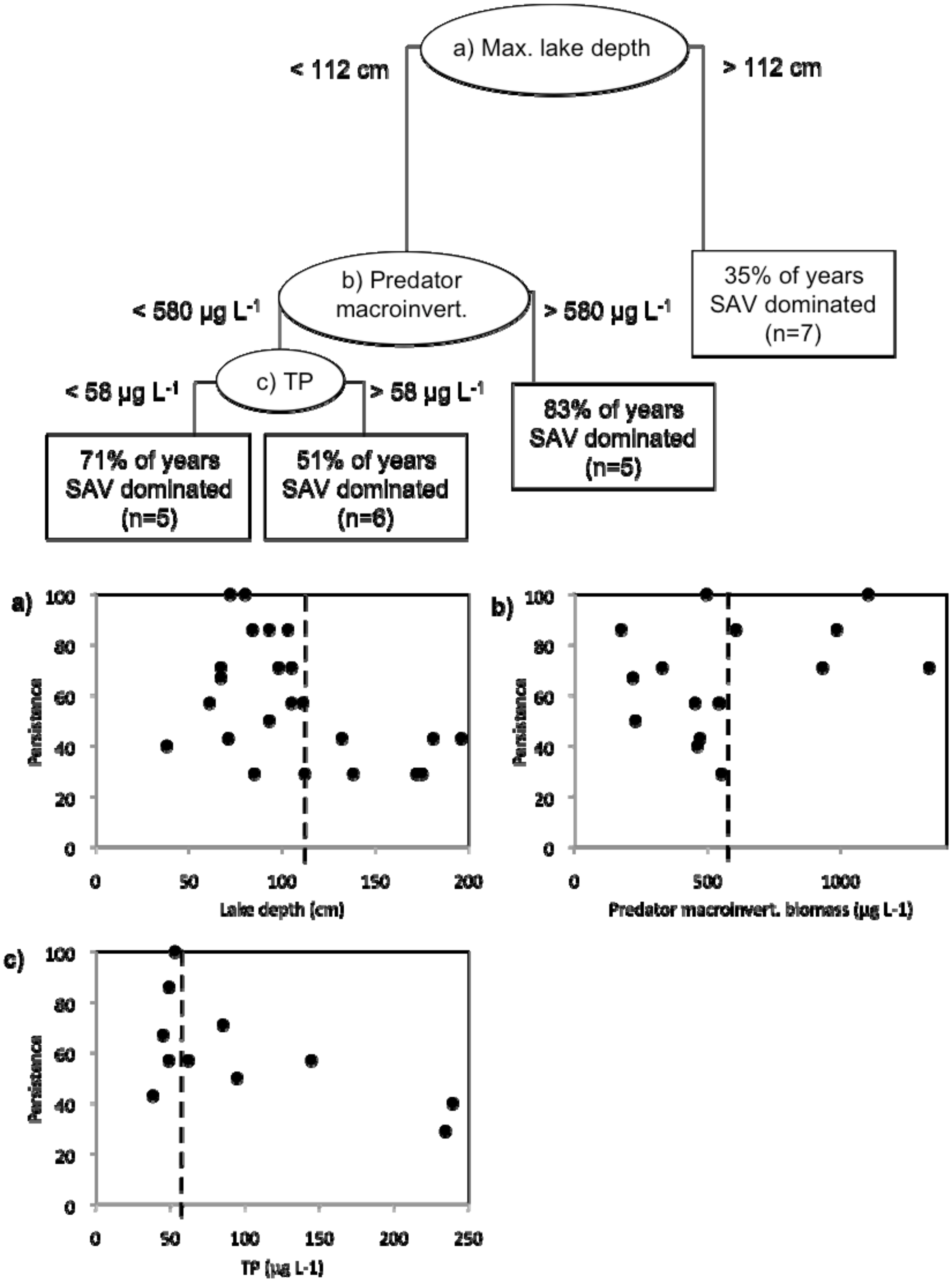

Figure 3-6. Regression tree predictions for the persistence of the SAV-rich regime based on within lake variables including max. lake depth, standard deviation in lake depth, TP, % Daphnia, predaceous macroinvertebrate biomass, total periphyton, and Cladocera/ chl-a ratio. The best model (variance explained = 0.66) included a) max. lake depth (R^2 = 0.21), b) predator macroinvertebrate biomass (R^2 = 0.10), and c) lake TP (R^2 = 0.38).

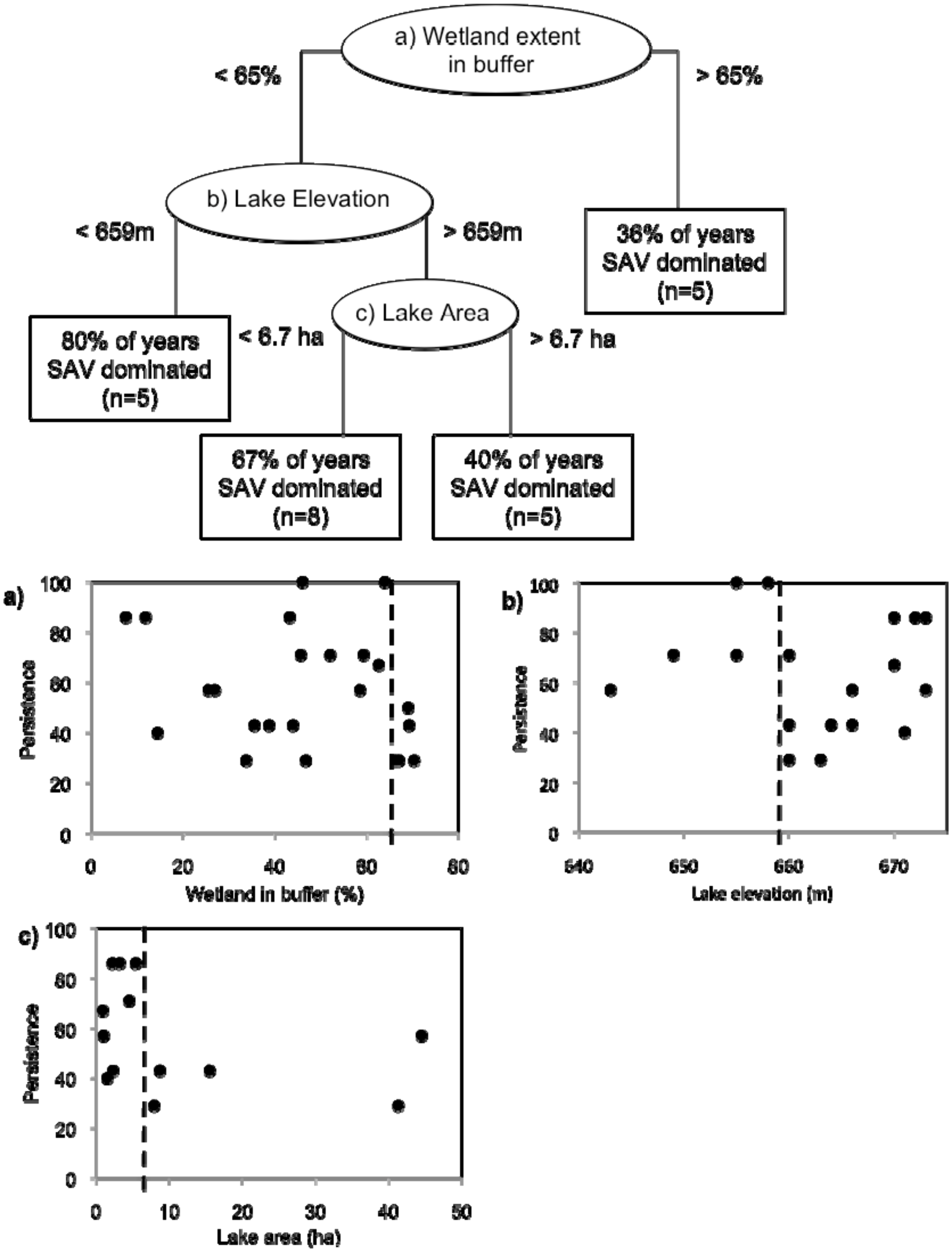

Figure 3-7. Regression tree predictions for the persistence of the SAV-rich regime based on landscape variables including including lake elevation, connectivity, % wetland in 300-m buffer, dominant surficial geology type, Ca + Mg, and lake area. The best model (total variance explained= 0.59) included a) wetland extent in the buffer (R^2 = 0.05), b) lake elevation (R^2 = 0.007), and c) lake area (R^2 = 0.09).

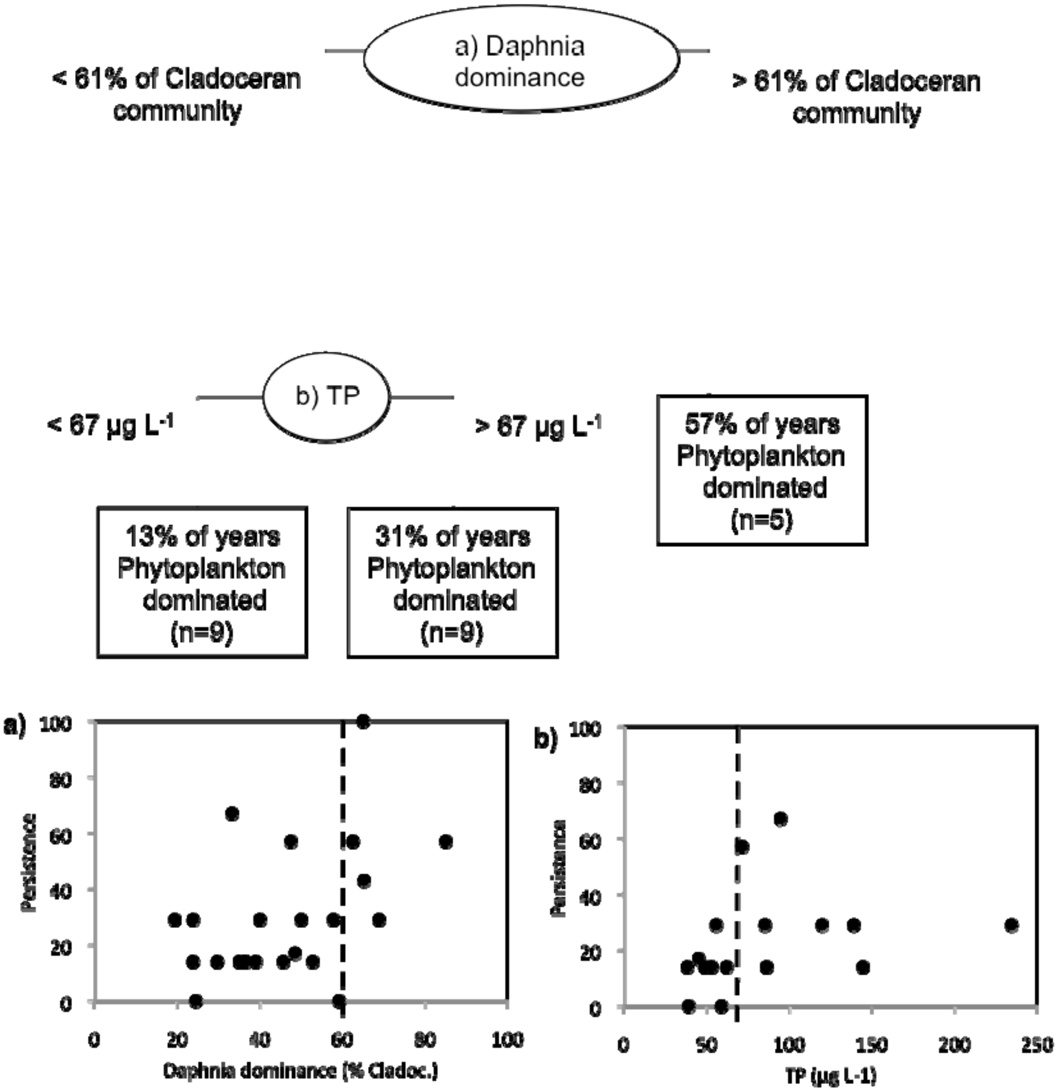

Figure 3-8. Regression tree predictions for the persistence of the phytoplankton-rich regime based on within lake variables including max. lake depth, standard deviation in lake depth, TP, % *Daphnia*, predaceous macroinvertebrate biomass, total periphyton, and Cladocera/ chl-a ratio. The best model (variance explained = 0.50) included a) *Daphnia* dominance (R^2 = 0.20), and b) lake TP (0.08).

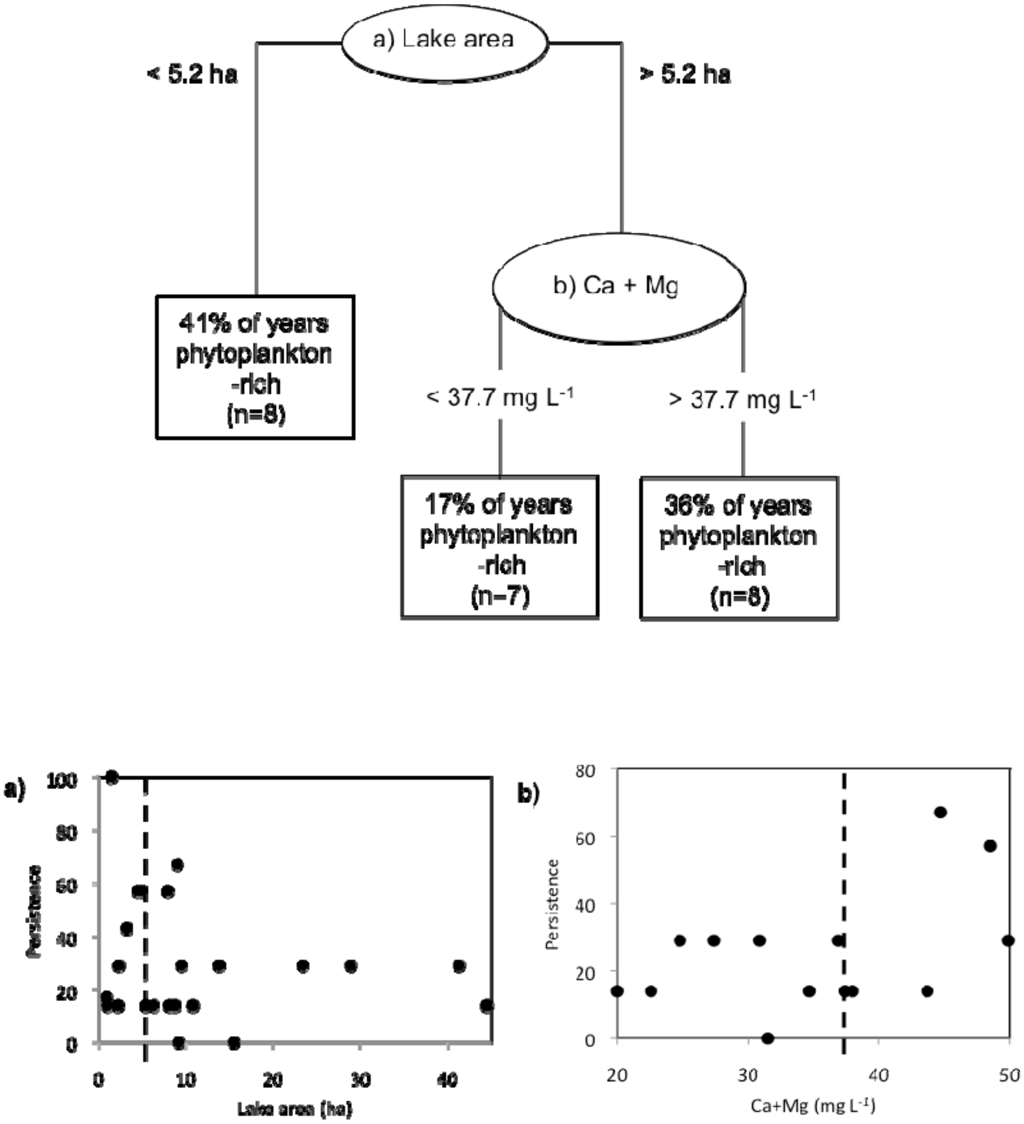

Figure 3-9. Regression tree predictions for the persistence of the phytoplankton-rich regime based on landscape variables including lake elevation, connectivity, % wetland in 300-m buffer, dominant surficial geology type, Ca + Mg, and lake area. The best model (total variance explained = 0.23) included a) lake area ($R^2 = 0.04$), and b) Ca + Mg ($R^2 = 0.31$).

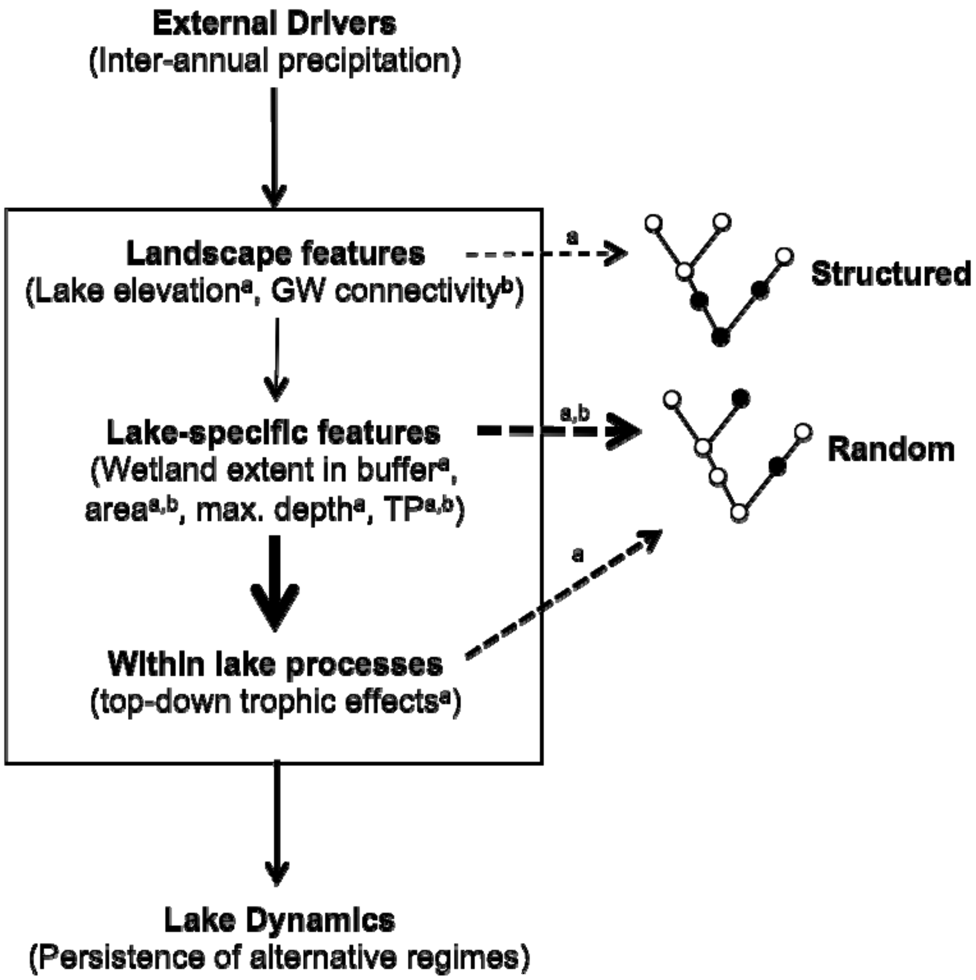

Figure 3-10. Diagram of hierarchy of controls on the persistence of alternative regimes and spatial patterns in lake dynamics generated at each level of control (modified from Kratz et al. 2005). Strongest control resides at the lake-specific level which results in the persistence of alternative regimes exhibiting a predominately random spatial pattern. The weight of the arrows indicates the relative strength of the controls. [a] and [b] indicates effects on the persistence of the SAV-rich regime and phytoplankton-rich regime, respectively.

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Chapter 4 - **Precipitation Induced Alternative Regime Switches in Shallow Lakes of the Boreal Plains (Alberta, Canada)**

Introduction

Shallow lakes are widely regarded as a classic example of ecosystems exhibiting alternative regimes. One regime is dominated by submersed aquatic vegetation (SAV) with clear water at low total phosphorus (TP) concentrations, and the other regime is dominated by phytoplankton with high turbidity at high TP concentrations, but at intermediate phosphorus concentrations either regime may exist (Scheffer et al. 1993). Previous studies have shown that alternative regimes are relatively persistent over time, with lakes in a clear or phytoplankton-dominated regime for several years to decades (Blindow et al. 1993; Scheffer et al. 1993; Hargeby et al. 2007). However, a recent study found that the majority of lakes in the Boreal Plains, Alberta, Canada exhibit highly unstable regimes, with 7% switching once and 73% switching 2-9 times over a 20-year period (Bayley et al. 2007). The high frequency of switches in a relatively pristine environment suggests that small perturbations in climate drive the switches, and the internal processes that maintain the clear or turbid state are weak (i.e. the states lack resilience).

Competitive interactions between SAV and phytoplankton for light and nutrients are thought to be the core mechanisms maintaining the alternative regimes in shallow lakes. Phytoplankton production decreases light penetration, limiting SAV growth below a (turbidity-dependent) depth and limiting lake coverage (Phillips et al. 1978; Eminson et al. 1980; Jeppesen et al. 1990; Scheffer et al. 1993). Because shallow lakes are often uniformly shallow, the exceedance of a turbidity threshold often results in the switching of an entire lake. Once a switch has occurred, the ecosystem may exhibit hysteresis, whereby the environmental conditions may need to be brought back further, beyond the switch point to return to normal (Scheffer et al. 2001; Scheffer et al. 2003). Clearly such ecosystems are challenging from a management perspective.

A suite of self-stabilizing mechanisms between SAV and phytoplankton and their environment are involved in maintaining the alternative regimes (reviewed by Scheffer and others. (1993)). SAV directly competes with phytoplankton for nutrients (Barko et al. 1998), and promotes water clarity through sediment stabilization by roots, providing habitat for zooplankton and invertebrate grazers, and supporting epiphyton that sequesters nutrients otherwise available to phytoplankton (Carpenter et al. 1986; Lauridsen et al. 1996). Perennial vegetative structures enable growth the following year further maintaining the clear state from year-to-year (Jeppesen et al. 1997). In contrast, when the same lakes may have high concentrations of nutrients, phytoplankton blooms appear to competitively exclude macrophytes through rapid nutrient uptake and re-release of phosphorus leading to algal blooms and shading (Jeppesen et al. 1997; Scheffer 1998). In the turbid state, fish are central to promoting a turbid state by recycling nutrients and controlling the development of zooplankton that could otherwise graze on phytoplankton. Fish and waves can also stir up sediments with little or no vegetation. Light limitation and disturbance of the sediments make it difficult for vegetation to establish (Jeppesen et al. 1997; Jeppesen et al. 1998; Scheffer 1998; Moss 2010).

Recent studies have focused on unravelling the mechanisms behind natural regime shifts in shallow lakes. Changes in water levels have been identified as a natural trigger for regime switches in shallow lakes. Water level decreases, particularly in nutrient-rich lakes, have generally been associated with increases in water clarity resulting in increased SAV coverage (Blindow et al. 1993; Van Geest et al. 2003; Van Geest et al. 2007), whereas water level increases tends to reduce light availability leading to decreased SAV coverage (Wallsten et al. 1989; Engel et al. 1994). Whether climate-mediated changes in lake depth may lead to switches in alternative regimes in shallow lakes on the Boreal Plains is unknown. A synoptic survey of boreal lakes suggests a water depth effect on the dominance of primary producers – the shallowest lakes supported high phytoplankton biomass and high SAV, lakes with moderate water levels were either clear with high SAV or turbid with low SAV depending on the TP levels, and the deepest lakes had low SAV and phytoplankton (Bayley et al. 2003). Vegetation growth models indicate that the range of nutrient levels with alternative states is much smaller in deeper water and eventually almost no vegetation growth occurs (van Nes et al. 2002). Furthermore, shallower lakes may freeze to the bottom, which may damage the over-wintering vegetative structures and weaken the persistence of SAV (Blindow et al. 1993). There is limited information on the extent that SAV is carried over from the previous year.

The hydrologic setting of shallow lakes in the Boreal Plains may make them sensitive to fluctuations in precipitation. The lakes are small, largely isolated, and the water budget is dominated by precipitation inputs (83 – 95%) and evaporative outputs (93 – 96%) (Ferone et al. 2004). Inter-annual differences in precipitation are likely to affect the concentration of nutrients and other limnological variables in these lakes. Lake water is naturally mesotrophic (median TP = 59.7 µg TP L^{-1}), reflecting shallow groundwater inputs from adjacent wetlands and peatlands (Ferone et al. 2004), whereas precipitation is nutrient-poor (Ferone 2001). Precipitation, even during storm events and the snowmelt period, results in little nutrient or organic matter runoff due to a terrain with low relief (elev. range = 643 – 673 m), a subhumid climate where precipitation is less than potential evapotranspiration,(Devito et al. 2005), high water storage capacity of wetlands and peatlands surrounding the lakes (Devito et al. 2005), and a high infiltration capacity of the underlying glacial sediments (Redding et al. 2008; Redding et al. 2011). This contrasts with lakes in a classic watershed model that receive high surface water inputs from upstream catchments during storm events, e.g. Schindler et al. (1996). In contrast to more human-affected lakes and watersheds in Europe (Wallsten et al. 1989; van Geest et al. 2003; van Geest et al. 2007), wetter conditions seem to lead to the dilution of chlorophyll-a in lakes on the Boreal Plains (Sass et al. 2008), which may increase water clarity and promote an SAV-rich regime.

This study aimed to identify how shallow lakes in the Boreal Plains respond to inter-annual fluctuations in precipitation, the key abiotic and biotic drivers of phytoplankton biomass and SAV abundance, and a mechanism for the frequent lake regime switches. I report on the inter-annual response of 23 lakes from 2001 to 2007. I explore the effect of fluctuations in annual precipitation on the regional lake response including water depth, nutrient concentration, turbidity, phytoplankton biomass, SAV abundance, and the percent of phytoplankton- and macrophyte-dominated lakes on the landscape. I studied many lakes over several years, creating a powerful approach that allowed us to assess shallow lake dynamics at a landscape scale.

I hypothesized that low annual precipitation would reduce lake levels, concentrating TP and leading to increased phytoplankton biomass (chl-*a*), higher turbidity, and decreased SAV cover. Wet years should increase lake levels, diluting TP, decreasing chl-*a* and turbidity, and favouring SAV growth.

Material and methods

The ecosystem

The study area is located approximately 370 km north of Edmonton, Alberta, Canada (56°6 N, 116 º32' W; Figure 4-1). It is part of the Boreal Plain ecozone of the Western Boreal Forest (extending across three provinces in west-central Canada). Long cold winters and short warm summers characterize the climate with average monthly temperatures ranging from -14.5 to 15.6 ºC for a mean annual temperature of 1.7ºC. The long-term (1971 – 2007) average annual precipitation is 466 mm, of which 59% falls during the growing season. The long-term maximum annual precipitation occurred in 1983 when 628 mm fell, whereas the lowest precipitation on record occurred in 1995, when only 89 mm fell (Environment Canada 2010). The lakes freeze in October – November, reaching an average ice depth of 50 to 75 cm by late winter, and generally thaw in April.

The terrain has low relief and is composed of glacially derived sediments overlying marine shales of the Upper Cretaceous Smoky Group (Hamilton et al. 1999). Surficial glacial sediments include glaciofluvial, glaciolacustrine, and moraine deposits from 40 to 240 m thick (Pawlowicz et al. 2002), resulting in complex surface water – groundwater interactions that do not necessarily reflect local surface topography (Devito et al. 2005). The landscape is generally pristine with minimal human influence, although oil and gas and forestry activities are present and expanding in the area.

The 23 study lakes were selected from a random population of shallow lakes in the study area such that there were approximately an equal number of lakes on each of the surficial geology types (i.e. a stratified random design). There were seven lakes on the glaciofluvial deposits, eight on the morainal deposits, and eight on the organic deposits. The lakes were small, ranging from 0.9 ha to 44.5 ha (mean ± stdev; 10.9 ± 12.1 ha), and shallow with flat bottoms. Average water depths ranging from 28 cm to 213 cm (83 ± 34 cm). The lakes are naturally mesotrophic with moderate concentrations of total phosphorus (median = 59.7 μg TP L^{-1}; 12.4 – 670.4 μg TP L^{-1}), nitrogen (median = 1990 μg TN L^{-1}; 618 – 5230 μg TN L^{-1}) and dissolved organic carbon (median = 39.5 mg DOC L^{-1}; 16.8 – 705.1 mg DOC L^{-1}) (Bayley et al. 2007). The water was typically phosphorus-limited with average total nitrogen to total phosphorus mass ratio of 17:1, and average available nitrogen to phosphorus ratio of 34:1 ([ammonium + nitrite-nitrate]: soluble reactive phosphorus). Algae grew quickly after ice-out and submerged macrophytes typically reach peak biomass in early August. Common primary producers included blue-green algae (primarily *Chroococcales* spp., *Microcystis* spp. and *Nostocales* spp.) and green algae (Chlorophyta), floating duckweeds (*Lemna minor* L. and *Spirodela polyrhiza* (L.) Schleid.) and submerged macrophytes (primarily *Myriophyllum sibiricum* Kom., *Ceratophyllum demersum* L., *Potamogeton friesii* Rupr., *P. richardsonii* (A. Benn.) Rydb. *P. zosteriformis* Fern., and *Drepanocladus aduncus* (Hedw.) Warnst.).

The zooplankton community was composed primarily of Cladocera (mean = 257.3 µg l^{-1}) and copepods (143.9 µg l^{-1}). The dominant Cladocera were *Daphnia dentifera* Forbes 1893 (formerly *D. rosea* G. O. Sars, 1862 (Taylor et al. 1996)) (82.8 µg l^{-1}), *D. pulex* Leydig, 1860 (26.8 µg l^{-1}), *Chydorus sphaericus* (O. F. Mueller, 1785) (51.9 µg l^{-1}), and *Ceriodaphnia quadrangula* (O. F. Müller, 1785). The dominant copepods were *Skistodiaptomus oregonensis* (Lilljeborg in Guerne and Richard, 1889) (25.2 µg l^{-1}) and *Macrocyclops albidus* (Jurine, 1820) (17.1 µg l^{-1}).

During the study period, 18 of the lakes lacked fish. Brook stickleback were observed in three of the lakes during all seven years, one lake in five years, and one lake in one year.

Lake survey

A survey of 23 lakes was conducted in early – mid August from 2001 to 2007, which coincided with peak SAV biomass. Physical, chemical and biological communities were sampled from three sites (nearshore, mid-width and centre) and pooled to estimate the overall lake conditions, unless otherwise stated. Physical factors measured included average water depth (typically n = 15), Secchi transparency and turbidity. Temperature, pH, dissolved oxygen, turbidity and electrical conductivity were measured in the field using a Hydrolab Quanta field probe (Hydrolab Corporation, Austin, Texas, U.S.A.). The water chemistry samples were collected with an integrated sampling tube, stored in dark bottles and kept cool (4º C) until they could be processed in the lab. Water chemistry analyses followed standardized procedures as described in Bayley and Prather (2003) for the following variables: phosphorus ([TP], total dissolved phosphorus [TDP], soluble reactive phosphorus [SRP]), nitrogen (total nitrogen [TN], total inorganic nitrogen [TIN], nitrate-nitrogen [NO_3^-], and ammonium-nitrogen [NH_4^+]), and dissolved organic carbon [DOC]. Chl-*a* was extracted with 95% ethanol and analyzed with a spectrophotometer at 750, 665, and 649 nm (Bergmann et al. 1980). Anions (chloride [Cl], sulphate [SO4]) and cations (sodium [Na], potassium [K], calcium [Ca], magnesium [Mg], iron [Fe] and silica [Si]) were analyzed only in 2001, 2002, 2003 and 2007.

SAV cover was estimated in each lake from 2001 to 2007. An overall lake assessment was based on 10 - 20 random quadrats. I used a ranked scale that ranged from 1 to 5, where S1 = little to no SAV cover (< 0.05%), S2 = sparse SAV cover (0.05 - < 5%), S3 = occasional plant cover (5 – < 25 %), S4 = common SAV cover (25 – < 75 %) and abundant SAV cover (75 – 100 %). The ranking included only SAV and excluded floating and emergent vegetation. This ranked scale was developed for aerial surveys of SAV coverage of shallow lakes in the region (Bayley et al. 2003; Bayley et al. 2007) and continued in this study. SAV biomass was sampled in each of the lakes from 2001 to 2004. I sampled SAV biomass using standardized rakes (1.00 x 0.38 m) from 20 random quadrats. The SAV biomass was stored in paper bags and dried at 65º C to constant weight (approximately 5 days). Regression analysis showed SAV cover ranks provide a reasonable and practical proxy for biomass in these lakes ($R^2 = 0.77$, $p < 0.0001$, n = 24 lakes) (Bayley et al. 2007).

Zooplankton samples (2 L) were collected with an acrylic tube (135 x 6.5 cm^2) (Swanson 1978), passed through 64-µm mesh netting, and preserved with a 4% formalin-sugar solution (Prepas 1978). Identification and enumeration methods are described by Norlin et al. (2005).

Fish presence was determined using a minimum of 10 Cuba Minnow Traps (Cuba Speciality Manufacturing, Fillmore, NY, U.S.A) placed at 5 – 10m intervals along a stretch of shoreline that were left overnight in each lake. Similar sampling methods have been used in other research on Brook stickleback populations (Moodie 1986).

Additionally, in August 2004 I assessed SAV biomass along a water depth gradient. I targeted the ten deepest lakes (average depth: 109 ± 30 cm; average maximum depth: 190 ± 58 cm) in the study region to maximize the water depth gradient. This included seven of the study lakes, and three additional lakes based on preliminary surveys that indicated the limnologic conditions and biological communities were similar to the study lakes. Above ground SAV biomass and water depth were sampled along three transects perpendicular to the shore using standardized rakes (1.00 x 0.38 m) from multiple sites (mean = 15 per lake; minimum = 12 per lake). SAV biomass samples were dried at 65º C to constant weight (approximately 5 days).

Data analysis

Effects of precipitation on lake conditions

I examined the relationships between the change in annual precipitation and change in annual lake conditions relative to the study period average. Annual precipitation was based on data from the Red Earth climate station (#3075488) (Environment Canada 2010), which was the only climate station in the study area. Annual precipitation from September through August of the survey year is the precipitation accumulated prior to and during the growing season of a given year. Annual lake conditions (lake depth, TP concentration, turbidity, chloride, phytoplankton biomass (chl-*a* concentration) and SAV abundance) are averages of the survey data from the 23 study lakes. Chloride is a conservative ion that is largely unaffected by food web effects, providing a useful indicator of the effects of precipitation on the concentration of solutes. Annual precipitation from only one regional climate station constrained the analysis to linear regression analysis between the annual average lake conditions (based on 23 lakes) and the annual precipitation of the region (based on one climate station), rather than a more robust test with the full lake data set. Similar analysis has been used in other studies of regional lake responses to climate (e.g. (Webster et al. 2000)).

I tested whether lake conditions differed among years using linear effects modelling (LME). Year was treated as a fixed effect, and lake (n = 23) as a random effect (i.e. lakes drawn at random from the population). Average lake conditions during the study period were used as a baseline for multiple comparisons (Dalgaard 2008).

I determined the percentage of lakes each year that were phytoplankton-rich and SAV-rich. SAV-rich was defined using a threshold value of >25% cover (SAV rating ≥ 3) based on previous studies in the region (Bayley et al. 2003). Other studies have observed a shift from a clear to turbid state associated with a threshold of > 20% cover (Van Geest et al. 2007) and > 30% cover (Jeppesen et al. 1990; Kosten et al. 2009) of lake surface area. Phytoplankton-rich was identified using a threshold chl-*a* concentration of 18 µg/L based on previous classification and analyses on lakes of the Boreal Plains (Bayley et al. 2007).

Statistical analyses were performed with R using the core package (R Development Core Team 2007) and the nlme package (Pinheiro et al. 2007).

Drivers of phytoplankton biomass and SAV coverage

I explored the key drivers affecting phytoplankton biomass and SAV abundance in these lakes to better understand the factors driving the switches between the alternative regimes. *A priori* hypotheses of lake factors that were considered plausible predictors of phytoplankton biomass and SAV coverage were developed (Anderson 2008) (Table 4-1). These hypotheses were tested using LME, which tests for linear relationships between the response and predictor variables while incorporating random effects and a model for error structure (i.e. temporal correlation) (Pinheiro et al. 2004). Lake was treated as a random effect, thus effectively removing the within-lake variability in the dataset from the analysis. The predictor variables were all continuous except fish presence or absence and year which were factors. Chl-*a* and other limnological variables were $\log_{10}(y+1)$ transformed to approximate normality.

First, I fit the data with a full fixed effect model (all potential fixed effect variables) and tested various variance-covariance structures. I tested an equal variance structure (equal variance – zero covariance), a serial correlation structure (equal variance – autoregressive covariance) and a variance structure for each year (varIdent – zero covariance). To account for serial correlation of observations from the same lake over years (i.e. repeated measures), I used an autoregressive function (AR1) that fits a parameter describing residuals whose correlation declines exponentially over time. The variance-covariance structures were fitted and compared by restricted maximum likelihood (REML) ratio tests (Pinheiro et al. 2004). Secondly, I fitted and compared the competing fixed effects models, which determined the key limnological variables driving the response variables. The full optimization maximum likelihood (ML) algorithm was used to fit and compare the fixed effects models, as recommended by Pinheiro and Bates (2004). Competing models were compared using delta Akaike's Information Criteria (ΔAIC) to determine which set of limnological factors best explained the response variables. AIC calculates the smallest subset of predictors that provides the best fit to the observed data (Pinheiro et al. 2004; Pinheiro et al. 2007). Thirdly, once the optimal model was found, it was fitted with REML and validated. I assessed residual versus fitted plots for homogeneity, histograms of residuals for normality, and residuals against explanatory variables to examine independence. Statistical analyses were performed with R using the core package (R Development Core Team 2007), the nlme package (Pinheiro et al. 2007), and the AICcmodavg package (Mazerolle 2010).

SAV biomass along a depth gradient

I was interested in the relationship between lake depth and SAV biomass to elucidate the SAV response to inter-annual variation in lake depth driven by precipitation. The relationship between SAV biomass and lake depth was examined using generalized additive mixed modelling (GAMM). GAMM was used because an initial linear regression model applied to the data showed residual patterns indicating non-linear relationships, which could not be corrected with data transformations (Zuur et al. 2009). A GAMM was fit with integrated smoothness estimate with a Gaussian distribution and identify link function and cross-validation to estimate the optimal amount of smoothing (Wood 2006; Zuur et al. 2009). Lake was treated as a random effect. Different variance-covariance structures were compared with AIC, and a simple variance structure was best (results not shown). Statistical analyses were performed with R using the core package (R Development Core Team 2007), the mgcv package (Wood 2010), and the AICcmodavg package (Mazerolle 2010).

Results

Precipitation quantities and lake conditions

Average annual precipitation was 376 mm, which was below the long-term average (1971 – 2007) of 466 mm. Water depth of the 23 study lakes averaged 82 cm during the study period and varied significantly between years (F=26.90; p-value = < 0.0001). Lake depth was lowest in 2002 (58 cm; P < 0.0001), and higher than average in 2005 (99 cm; P = 0.0002), 2006 (104 cm; P = < 0.0001), and 2007 (95 cm; P = 0.003). During the study TP averaged 81.8 µg L^{-1}, turbidity averaged 3.9 NTU, phytoplankton biomass averaged 16.9 µg Chl-a L^{-1}, and SAV cover averaged 3.2 SAV rating (equivalent to 25 to 75% cover). The majority of lakes during the study were macrophyte-dominated (average = 62%), whereas only 28% of lakes were phytoplankton-dominated. Brook stickleback was observed in three of the lakes during all seven years, in one lake for five years, and one lake for one year and were absent in 17 lakes.

Precipitation was lowest in 2002 (227 mm), which coincided with the lowest lake levels (mean = 58 cm), the highest concentrations of TP (109.3 µg L^{-1}), chl-*a* (18.0 µg Chl-a L^{-1}), chloride (3.3 mg Cl L^{-1}), and turbidity (13.5 NTU), and the lowest abundance of SAV (2.8 ± 0.3 SAV rating; 5 to 25% cover). In 2002, forty-three percent of the lakes were phytoplankton dominated, the highest proportion of the years studied. Forty-three percent of lakes were also SAV-dominated, the lowest of the years studied.

The wettest year occurred in 2005 with two times greater (500 mm) precipitation than in 2002. Average lake levels were high (99 cm), and TP (43.1

$\mu g \ L^{-1}$), chl-a concentrations (6.3 $\mu g \ L^{-1}$), and turbidity levels (1.4 NTU) were low. In 2005, only five percent of lakes were phytoplankton dominated; the lowest recorded. Fifty-five percent of lakes were SAV dominated – an increase from the previous year but below average for the study period. Water levels remained high in 2006 and 2007, coinciding with an increasing percentage of lakes that were SAV dominant, reaching a maximum of ninety percent in 2007.

Relationships between precipitation and lake conditions

Increases in annual precipitation (relative to the study period average) was associated with decreased TP, chl-*a*, and turbidity concentrations (Figures 4-2a – c). These relationships were significant explaining 68% of the variation in the TP concentration ($F_{1,5} = 10.51$, $P = 0.023$), 87% of the variation in the chl-*a* concentration ($F_{1,5} = 33.93$, $P = 0.002$), and 70% of the variation in turbidity values ($F_{1,5} = 11.7$, $P = 0.019$). Chloride concentration decreased with increased precipitation, explaining 73% of the variance, although the result was not significant due to a small sample size ($n = 4$; $P = 0.14$). Lake depth increased with annual precipitation, although the relationship was not statistically significant ($R^2 = 0.38$; $F_{1,5} = 3.08$, $P = 0.14$).

Change in lake depth was a better predictor than change in annual precipitation of SAV cover and biomass. Change in lake depth explained 27% of the variance in SAV cover (Figure 4-3a), compared to change in annual precipitation, which only explained 6% of the variance. Neither relationship was statistically significant ($F_{1,5} = 1.84$, $P = 0.23$; and $F_{1,5} = 0.32$, $P = 0.59$, respectively). I also examined the relationships between SAV biomass and change in annual precipitation and change in lake depth from 2001 to 2004 (only years sampled). Positive changes in lake depth (relative to the study period average) was positively associated with SAV biomass, explaining 97% of the variance in the data ($F_{1,5} = 59.47$, $P = 0.016$; Figure 4-3b). Change in annual precipitation explained 59% of the variance in SAV biomass; however this relationship was not statistically significant ($F_{1,5} = 2.63$, $P = 0.25$).

Factors driving phytoplankton biomass

Phytoplankton biomass was best predicted by TP concentration, which was highly significant ($F = 58.69$; $P = < 0.0001$) and *Daphnia* biomass (Table 4-2, Model 10). Chl-*a* increased linearly with TP concentration ($ß = 0.85 \pm 0.11$; $P < 0.0001$). There was high variance in the relationship at high TP and chl-*a* values, based on the confidence intervals around the mean ($ß = 6.14$, min. 95% C.I. = 2.87; max. 95% C.I. = 4.81). *Daphnia* biomass contributed to the model, although the Chl-*a* – *Daphnia* relationship was not statistically significant ($F = 1.49$; $P = 0.23$). *Daphnia* had a weak negative relationship with phytoplankton biomass ($ß = -0.10 \pm 0.16$).

Phytoplankton biomass was best modelled with an equal variance structure (Table 4-2, Model 1) indicating a lack of auto-correlation in the data. Initially the best fixed effects model included TP, *Daphnia* and Year (Table 4-2, Model 4). Further model testing indicated that Year could be dropped from the model.

Factors driving SAV cover

Turbidity ($F = 11.09$, $P = 0.0013$), the previous year's SAV cover ($F = 18.70$, $P < 0.0001$), and year ($F = 3.23$; $P = 0.0065$) all contributed significantly to the best SAV model (Table 4-3, Model 4). The weight of evidence was only 1.2X greater than the same model including water depth (Table 4-3, Model 5), suggesting that water depth may be a tertiary factor affecting SAV cover.

The previous year's SAV cover was an important factor predicting the current year's coverage and the relationship was highly significant ($P = 0.0001$; $\beta = 0.35$, upper 95% C.I. = 0.51, lower 95% C.I. = 0.18). This result, combined with temporal correlation in the data structure (Table 4-3, Model 2), indicates that SAV is not reset each year. Overall, there were large inter-annual differences in SAV cover. SAV cover tended to decrease from the previous year in 2002, and tended to increase from the previous year in 2006 and 2007. Turbidity had a negative effect on SAV cover, although the slope was not significant ($P = 0.30$; $\beta = -0.33$, upper 95% C.I. = 0.30, lower 95% C.I. = -0.96).

SAV biomass along a water depth gradient

SAV biomass followed a unimodal pattern along a water depth gradient, peak SAV biomass occurred at approximately 125 cm with lower SAV biomass at shallower and deeper sites (Figure 4-4a). There was little SAV biomass beyond 175 cm depth (Figure 4-4b). The regression fit was significant ($F = 3.28$; $P = 0.036$) with two degrees of freedom providing the best balance between fit and smoothness. SAV biomass was highly variable with only five percent of the variance explained by water depth ($R^2 = 0.05$), in part due to the high number of quadrats along the water depth gradient that were absent of SAV biomass.

Discussion

Fluctuations in precipitation driving regime shifts

Fluctuations in annual precipitation levels affected the competitive interactions between phytoplankton and SAV for nutrients and light driving inter-annual shifts in alternative regimes in shallow lakes of the Boreal Plains. Low annual precipitation concentrated TP, chloride, phytoplankton biomass and organic matter in the water column shading SAV and promoting a turbid, phytoplankton-rich state. During wet periods precipitation diluted solutes in the water column, promoting a clear water, SAV-rich state (Figure 5).

Shallow lakes of the Boreal Plains are sensitive to fluctuations in precipitation. The lakes are small, shallow, isolated, and the hydrologic budget is dominated by precipitation inputs (83 – 95%) and evaporative outputs (93 – 96%), with little fluxes from groundwater or surface water runoff (Ferone et al. 2004). Lake water on the Boreal Plains is nutrient-rich reflecting mesic peat and gyttja water sources from shallow groundwater inputs (Ferone et al. 2004), whereas precipitation is nutrient poor (Ferone 2001). The concentration effect from evaporation will create a situation in which organic matter and nutrients from decaying plants, dissolved organic matter, and phytoplankton accumulate in the water column. Added to this, repetitive wave re-suspension over large areas is common in shallower lakes (Bloesch 1995). During the drought, turbidity levels were 3X higher than the previous year whereas chl-*a* was only 1.5X greater, suggesting that sediment re-suspension may play a role. Evaporative concentration of nutrients and organic matter in isolated lakes is an important mechanism influencing phytoplankton production, as seen in other boreal (Schindler et al. 1996) and floodplain lakes (Sokal et al. 2008; Loverde-Oliveira et al. 2009; McGowan et al. 2011).

Precipitation inputs had strong effects on nutrient and turbidity levels, but did not have a strong relationship with lake depth. Increased precipitation on the Boreal Plains often increases lake area rather than depth, and adjacent upland soil storage and peatland complexes attenuate lake levels and storage responses (Ferone et al. 2004; Devito et al. 2005; Redding et al. 2010).

Annual macrophyte abundance was better predicted by change in annual lake depth rather than change in annual precipitation quantities. Macrophytes have relatively slow population dynamics compared to phytoplankton and their growth in a given year is a function of water clarity (dependent on water depth and turbidity) and SAV abundance from the previous year. During the study SAV cover increased with lake depth and was significantly higher in 2007 following 3 years of higher water levels. However, the study period was relatively dry; average annual precipitation was 90 mm below the 30-year average. During this time lake depth averaged 83 cm, peaking in 2006 at 104 cm. The SAV biomass – lake depth study indicates a unimodal relationship peaking at 125cm. SAV growth is presumably limited at shallower depths (< 125cm) by increased turbidity, and at deeper depths (> 125cm) by light attenuation due to increasing water depth. There was little SAV biomass beyond 175cm depth. If wetter conditions return, similar to the long-term average, deeper lakes (> 175 cm) will likely exhibit a clear regime with low phytoplankton biomass and low macrophyte coverage (Figure 6). Such a regime has been observed in deeper lakes in a large synoptic survey of the region (Bayley et al. 2003).

Climate-induced changes in lake depth has been observed as a natural shifting mechanism in other shallow lakes. Similar to the study lakes, increased water levels have been associated with increased water clarity, decreased phytoplankton biomass (Noges et al. 1999) and promotion of an SAV dominant state (Loverde-Oliveira et al. 2009). However, lakes of the Rhine River floodplain differed fundamentally in their response to reduced water levels. Presumably, lowered water levels improved light conditions sufficiently for SAV establishment, triggering a switch from a stable turbid state to an unstable clear state (Van Geest et al. 2007). As most of the lakes of the Rhine floodplain are nutrient-rich (220 μg TP L^{-1} versus 82 μg TP L^{-1} on the Boreal Plains), these lakes are assumed to be stable only in the turbid state. Similar to lakes of the Boreal Plains, those on the Rhine floodplains displayed strong and frequent inter-annual switches associated with fluctuations in water levels. The SAV-rich state displayed resilience in some lakes over several years even following a return to turbid conditions. This co-dominant state was characterized as a 'ghost' of the SAV-rich equilibrium (Van Geest et al. 2007).

This study focused on the regional lake response to inter-annual variations in climate. The sensitivity of lakes within the region to fluctuations in precipitation is likely to vary based on differences in hydrologic setting. The hydrologic setting of shallow lakes in the Boreal Plains is highly variable due to deep glaciated substrates that result in complex surface and groundwater interactions

(Devito et al. 2005). Variations in surficial geology, the proportion of wetland versus upland in the watershed, local topography and lake morphometry alters the dominant water fluxes (proportion of atmospheric, surface water and ground water), chemical properties (e.g. TP levels), and susceptibility of the lakes to changes in climate (Devito et al. 2000; Ferone et al. 2004; Devito et al. 2005). Future studies should examine how lakes within the region differ in their sensitivity to switching alternative regimes to determine which landscape features are important.

Implications for alternative state theory in shallow lakes

This study indicates that fluctuations in precipitation can cause frequent switches in ecosystem regimes in shallow lakes. This differs from the archetypical image of shallow lakes that exhibit an alternative regime for several years to decades, and switches only occur following a strong perturbation (Blindow et al. 1993; Scheffer et al. 1993). The conception and development of the theory of alternative stable states in shallow lakes has been based primarily on lakes in a temperate climate in Europe and North America. These lakes typically have low nutrient levels and a rich fish community in their pristine state. Lake regime switches have most often been associated with severe perturbations, including human-induced eutrophication, severe changes to lake levels, or changes to the fish community. In contrast, shallow lakes on the Boreal Plains of Canada are predominately fishless with little top-down control, the landscape setting supports lakes that are sensitive to fluctuations in precipitation, and they are subject to harsh climatic conditions. Under these conditions, disturbances are the rule rather than the exception. Such systems will be transient and far from equilibrium most of the time (Hastings 2004).

Only the clear, SAV-dominated regime has resilience from year-to-year in shallow lakes on the Boreal Plains. During the study 61% of lakes were SAV dominant compared to only 30% of lakes that were phytoplankton dominant. SAV cover was temporally correlated and a significant predictor of SAV cover the following year. SAV abundance only showed a significant increase in 2007, following 3 years of high water levels. Additionally, a broader study of lakes in the region found that over a 20-year period of all the lakes that were stable (20%) were clear, with mesotrophic TP concentrations (median = 39.2 μg/L) (Bayley et al. 2007). In contrast, phytoplankton exhibited little "memory" from year-to-year. There were strong and frequent inter-annual shifts in phytoplankton biomass associated with fluctuating precipitation levels. Drought appears to switch the lakes from a relatively stable, clear, SAV-rich regime into an unstable phytoplankton-rich regime. The perennial nature and relatively slow growth habit of many SAV species imparts resilience to the regime. Vegetated lakes are likely to remain so because vegetation can be gained and lost gradually in the shallower and deeper parts of the lake (Amemiya et al. 2007), and plants are less affected by turbidity at shallower sites (van Nes et al. 2002). Furthermore, SAV appears to withstand turbid conditions in shallower lakes on the Boreal Plains. A high SAV and high phytoplankton regime were observed in the shallowest lakes in a synoptic survey of the region (Bayley et al. 2003). The tendency for higher resilience of the clear state has been suggested in other studies of shallow lakes (Hargeby et al. 2007).

Coupling the quick population dynamics of phytoplankton and slower population dynamics of SAV illustrates the dominant role that transient dynamics play in understanding this system (Hastings 2004). This study also emphasizes the importance of monitoring complex ecological systems over longer time periods to better understand the mechanisms for natural regime shifts and their frequency.

Management implications

Evidence of strong relationships between precipitation quantities and limnological properties provides a basis for predicting the ecological responses of shallow lakes to future hydrologic change. This study suggests that shallow lakes of the Boreal Plain are sensitive to changes in water inputs that may occur due to future climate change and anthropogenic water withdrawals. The study region has undergone a warming of 2.2°C and change in annual precipitation of -146.5 mm since 1970 (Schindler et al. 2006). If both of these trends continue lake levels will decrease promoting a turbid water regime. Additionally, the oil and gas industry is active throughout the Boreal Plains of western Canada, and water withdrawals associated with these activities has the potential to elevate algal production and decrease SAV abundance in shallow lakes. However, provided these are short-term disturbances and the system is not subject to hysteresis, the system may revert back to its natural structure and processes fairly quickly. This contrasts with relatively stable regimes observed in other shallow lakes systems, where restoring a desired state may require drastic and expensive restoration.

Tables

Table 4-1. *A priori* set of hypotheses of limnological factors driving phytoplankton biomass and submerged aquatic vegetation cover.

Phytoplankton biomass	
TP	TP is the main nutrient limiting phytoplankton biomass (+ effect).
TP + Water depth	Phytoplankton biomass responds to the interaction between water depth and TP. Low water depth concentrates TP (+ effect) and high water depth dilutes TP (- effect). However, deep lakes favour fish, which are predicted to promote chl-a (+ effect).
TP + Water depth + Fish	Same as above, except fish prey on large zooplankton biomass, increase re-suspension of nutrient rich sediments, and have high TP recycling rates (+ effects).
TP + Daphnia	Same as above, except Daphnia grazer effects (- effect). (Jeppesen et al., 1999)
TP + Daphnia + Fish	Combination of above factors.
TP + Water depth + Daphnia	Combination of above factors.
TP + Water depth + Daphnia + Fish	Combination of above factors.
Submerged aquatic vegetation cover	
Turbidity	Decreased light transparency shades SAV, includes chl-a and other organic and inorganic matter. (- effect)
Chl-a	Limits light availability and shades SAV. (- effect) Does not include other detritus and inorganic matter.
TP	Decreased transparency due to increased algal growth or higher concentrations of suspended sediments. (- effect)
Water depth	Water depth reduces light penetration to the lake bottom.
SAV$_{(Y-1)}$	SAV is not reset each year. The SAV cover from the previous year contributes to the next years growth.
Turbidity + Water depth	Decreased water levels increases turbidity (- effect) because nutrients and organic matter are concentrated. Also, shallower lakes may have higher metabolic activity resulting in increased plant decomposition and higher inputs of organic matter and nutrients.
Turbidity + SAV$_{(Y-1)}$	Combination of above factors.
Turbidity + Water depth + SAV$_{(Y-1)}$	Combination of above factors.

Table 4-2. Factors driving phytoplankton biomass (chl-*a*) from 2001 to 2007 in the 23 study lakes based on LME analysis.

Model	Fixed effects	Variance- covariance structure	Estim. method	K	AICc	Δ_i	w_i
Testing variance – covariance structure							
1	TP + *Daphnia* + Water depth + Fish + Year	Equal var – Zero cov	REML	12	166.56	0.00	0.70
2	TP + *Daphnia* + Water depth + Fish + Year	Equal var – corAR1	REML	13	168.44	1.88	0.27
3	TP + *Daphnia* + Water depth + Fish + Year	varIdent – Zero cov	REML	17	173.36	6.80	0.02
Initial selection of fixed effects variables							
4	TP + *Daphnia* + Year	Equal var – Zero cov	ML	10	123.75	0.00	0.64
5	TP + *Daphnia* + Fish + Year	Equal var – Zero cov	ML	11	124.90	1.15	0.27
6	TP + *Daphnia* + Water depth + Year	Equal var – Zero cov	ML	11	125.72	1.97	0.18
7	TP + *Daphnia* + Water depth + Fish + Year	Equal var – Zero cov	ML	12	127.10	3.35	0.09
8	TP + Year	Equal var – Zero cov	ML	10	138.21	14.46	0.00
9	TP + Water depth + Year	Equal var – Zero cov	ML	11	140.27	16.52	0.00
10	TP + Water depth + Fish + Year	Equal var – Zero cov	ML	12	140.30	16.55	0.00
Final selection of fixed effects variables							
4	TP + *Daphnia* + Year	Equal var – Zero cov	ML	10	123.75	6.96	0.03
10	TP + *Daphnia*	Equal var – Zero cov	ML	5	116.80	0.00	0.97

The phytoplankton biomass (Log chl-a) model selection procedure. A priori models were tested to determine the best (lowest AIC value) variance-covariance structure and fixed effects variables. Year (2001 – 2007) was treated as a fixed effect variable. Lake (n =23) was treated as a random variable with fitted intercepts. Zero cov specifies random variance structure (i.e. no temporal correlation). CorAR1 specifies residual correlation that decays exponentially with distance between time periods (i.e. years). VarIdent specifies separate error terms for each Year (i.e. heteroscedasticity). The number of parameters in the model (K), the AICc, change in AICc (i = AICci - AICcmin), and normalized Akaike's weights (wi) are shown. The final phytoplankton biomass (chl-a) model coefficients (± SE) are intercept = -0.41 ± 0.22 (P = 0.07), Log TP = 0.85 ± 0.11 (P < 0.0001), Log Daphnia = -0.05 ± 0.04 (P = 0.23).

Table 4-3. Factors driving macrophyte cover from 2001 to 2007 in the 23 study lakes based on LME analysis.

Model	Fixed effects	Variance- covariance structure	Estim. method	K	AICc	Δ_i	w_i
Selecting variance – covariance structure							
1	Turbidity + Water depth + SAV$_{(Y-1)}$ + Year	Equal var – Zero cov	REML	12	378.27	4.94	0.08
2	Turbidity + Water depth + SAV$_{(Y-1)}$ + Year	Equal var – corAR1	REML	13	373.33	0.00	0.92
3	Turbidity + Water depth + SAV$_{(Y-1)}$ + Year	varIdent – Zero cov	REML	18	391.20	17.87	0.00
Initial selection of fixed effects variables							
4	Turbidity + SAV$_{(Y-1)}$ + Year	Equal var – corAR1	ML	12	352.70	0.00	0.54
5	Turbidity + SAV$_{(Y-1)}$ + Water depth + Year	Equal var – corAR1	ML	13	353.05	0.35	0.46
6	Turbidity + Year	Equal var – corAR1	ML	11	409.91	57.21	0.00
7	Turbidity + Water depth + Year	Equal var – corAR1	ML	12	411.33	58.62	0.00
8	SAV$_{(Y-1)}$ + Year	Equal var – corAR1	ML	11	433.73	81.02	0.00
9	Chl-*a* + Year	Equal var – corAR1	ML	11	458.44	105.74	0.00
10	TP + Year	Equal var – corAR1	ML	11	463.59	110.89	0.00
11	Water depth + Year	Equal var – corAR1	ML	11	474.95	122.25	0.00
Final selection of fixed effects variables							
4	Turbidity + SAV$_{(Y-1)}$ + Year	Equal var – corAR1	ML	12	352.70	0.00	0.94
12	Turbidity + SAV$_{(Y-1)}$	Equal var – corAR1	ML	6	358.07	5.37	0.06

The SAV cover model selection procedure. A priori models were tested to determine the best (lowest AIC value) variance-covariance structure and fixed effects variables. Year (2001 – 2007) was treated as a fixed effect variable. Lake (n =23) was treated as a random variable with fitted intercepts. Zero cov specifies random variance structure (i.e. no temporal correlation). CorAR1 specifies residual correlation that decays exponentially with distance between time periods (i.e. years). VarIdent specifies separate error terms for each Year (i.e. heteroscedasticity). The number of parameters in the model (K), the AICc, change in AICc (i = AICci - AICcmin), and normalized Akaike's weights (wi) are shown. The final SAV cover model coefficients (± SE) are intercept = 2.1 ± 0.47 (P < 0.0000), Log Turbidity = -0.33 ± 0.32 (P = 0.30), SAV(Y-1) = 0.35 ± 0.08 (P = 0.0001).

Figures

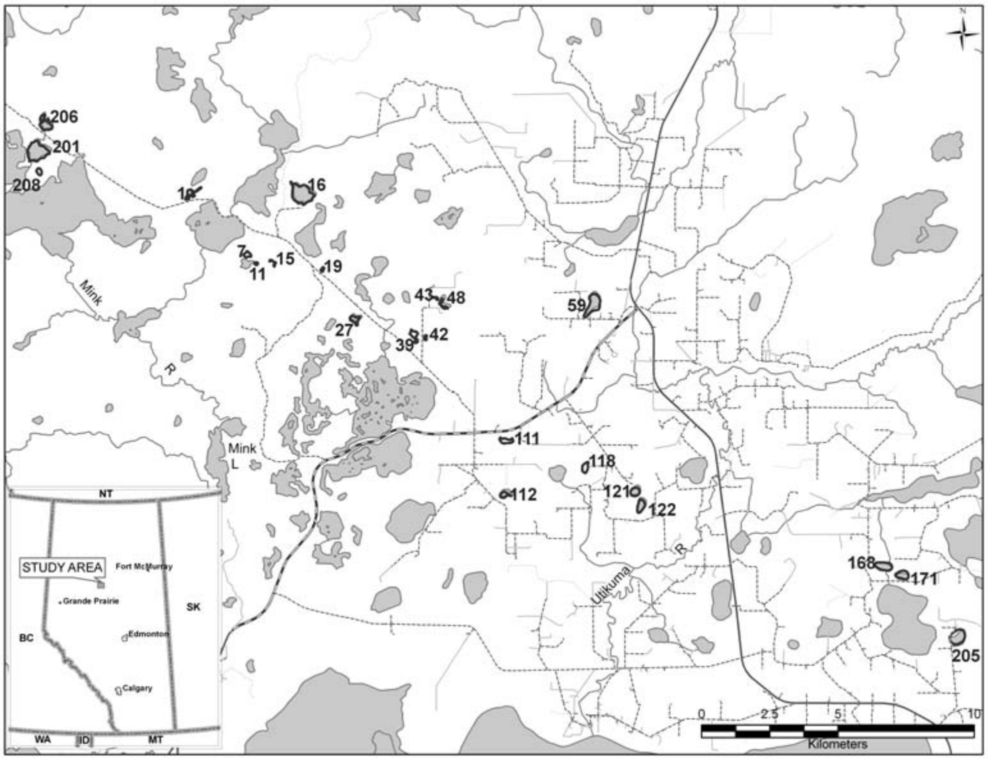
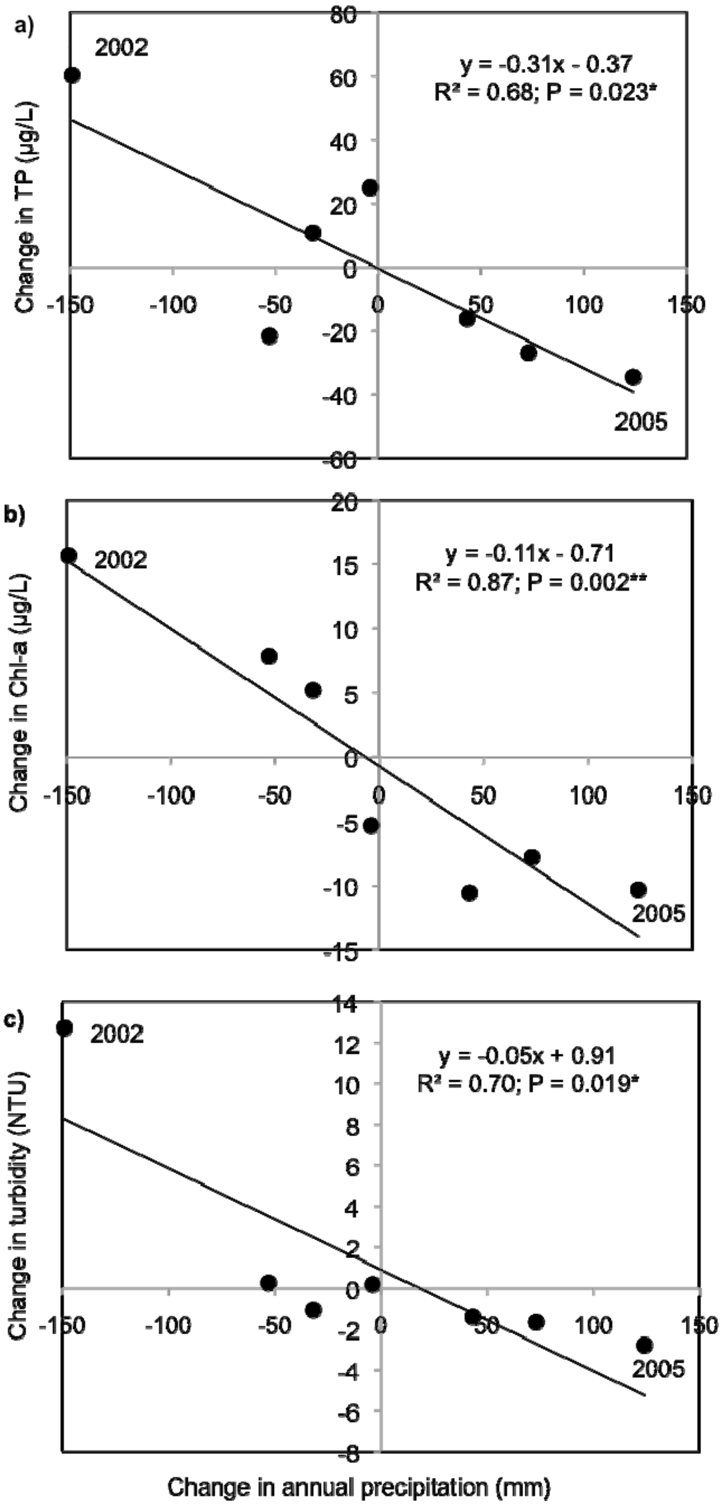


Figure 4-1. Location of the 23 study lakes.


a)
2002
y = -0.31x - 0.37
R² = 0.68; P = 0.023*
2005
Change in TP (µg/L)
80
60
40
20
0
-20
-40
-60
-150
-100
-50
0
50
100
150
b)
2002
y = -0.11x - 0.71
R² = 0.87; P = 0.002**
2005
Change in Chl-a (µg/L)
20
15
10
5
0
-5
-10
-15
-150
-100
-50
0
50
100
150
c)
2002
y = -0.05x + 0.91
R² = 0.70; P = 0.019*
2005
Change in turbidity (NTU)
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-150
-100
-50
0
50
100
150
Change in annual precipitation (mm)

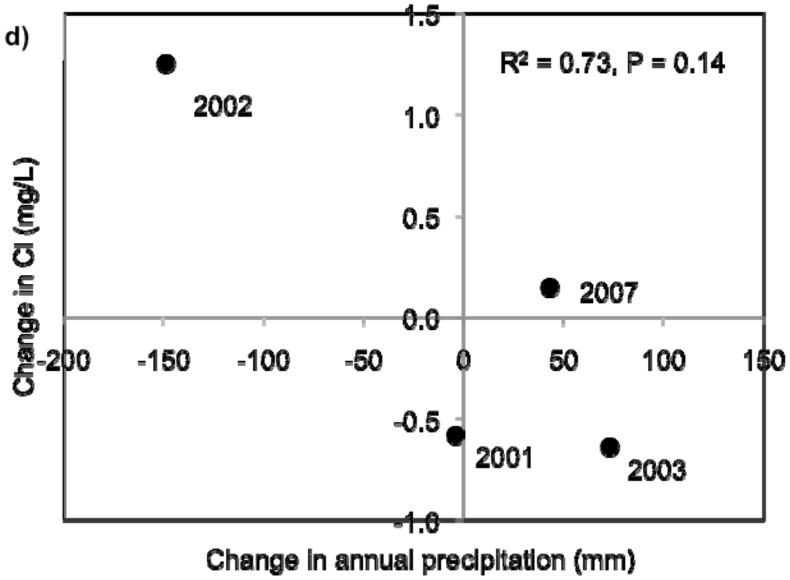


Figure 4-2. Relationships between annual change in precipitation and annual change in a) TP; b) chl-a; c) turbidity and d) chloride concentrations. Annual TP, chl-a, turbidity and chloride values are averages based on survey data from 23 lakes. Changes are deviance from the study period average.

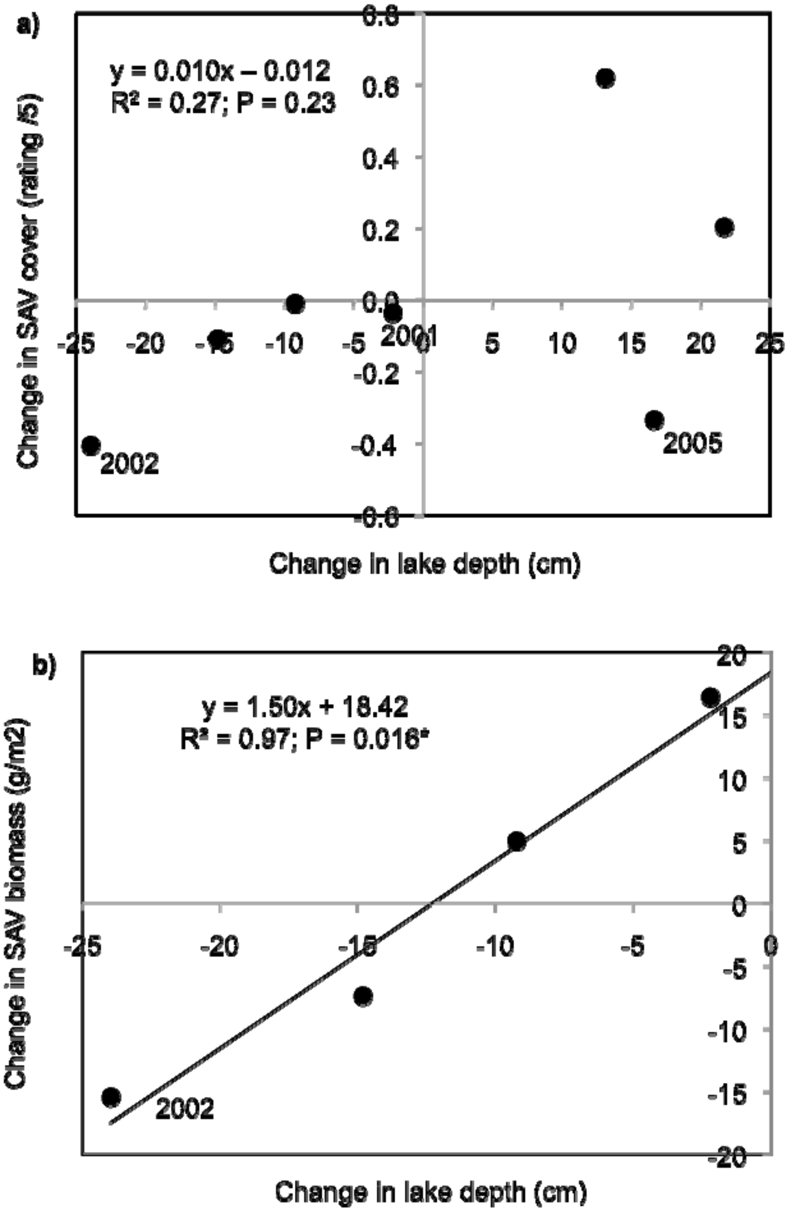


Figure 4-3. Relationships between annual change in lake depth and annual change in a) SAV cover from 2001 to 2007; and b) annual SAV biomass from 2001 to 2004 (only years studied). Annual values are averages based on survey data from 23 lakes. Changes are deviance from the study period average.

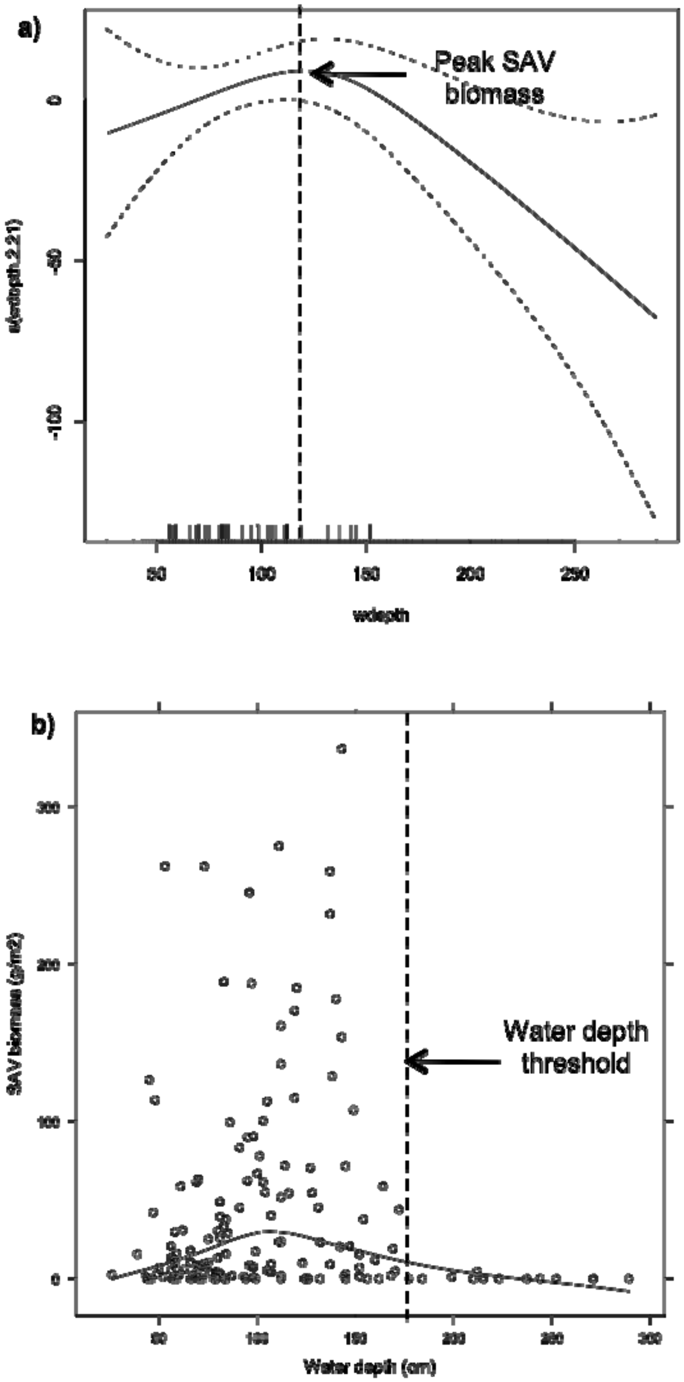


Figure 4-4. Relationship between water depth (cm) and SAV biomass showing the a) predicted SAV biomass from GAMM analysis indicating peak biomass at 125 cm depth, and b) raw data showing little occurrence of SAV biomass beyond 175 cm depth. Data are based on 12-15 sites nested within 10 lakes.

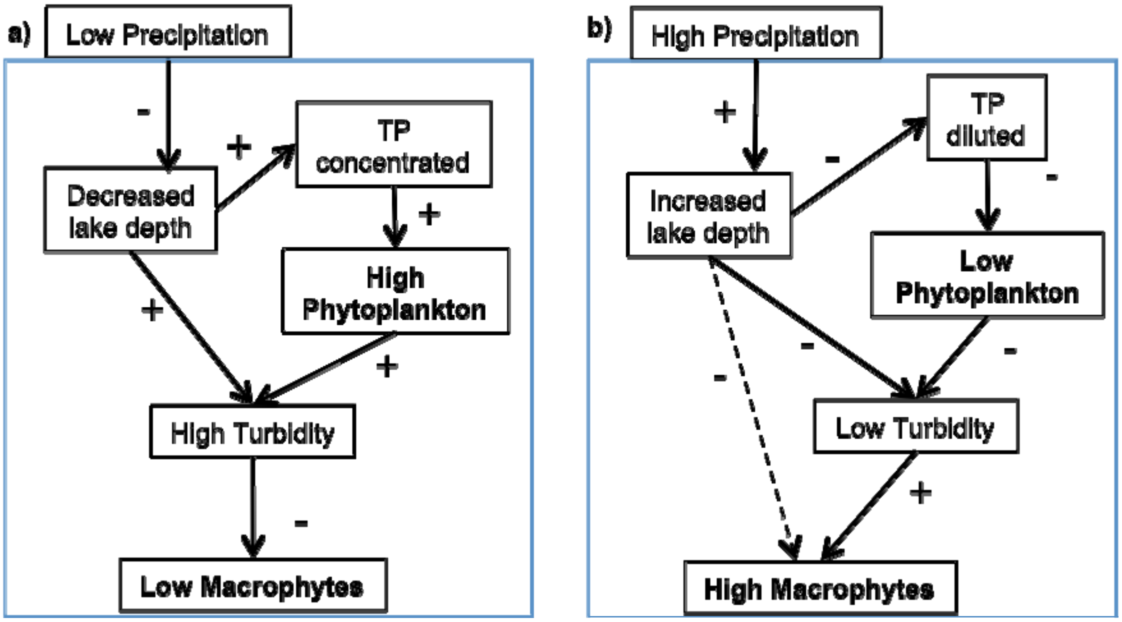


Figure 4-5. Conceptual model whereby a) low precipitation promotes a turbid, high phytoplankton regime, and b) high precipitation promotes a clear, high macrophyte regime. The dashed line indicates the predicted negative effects of water depth on macrophytes abundance in very wet years (i.e. water depth > 125 cm).

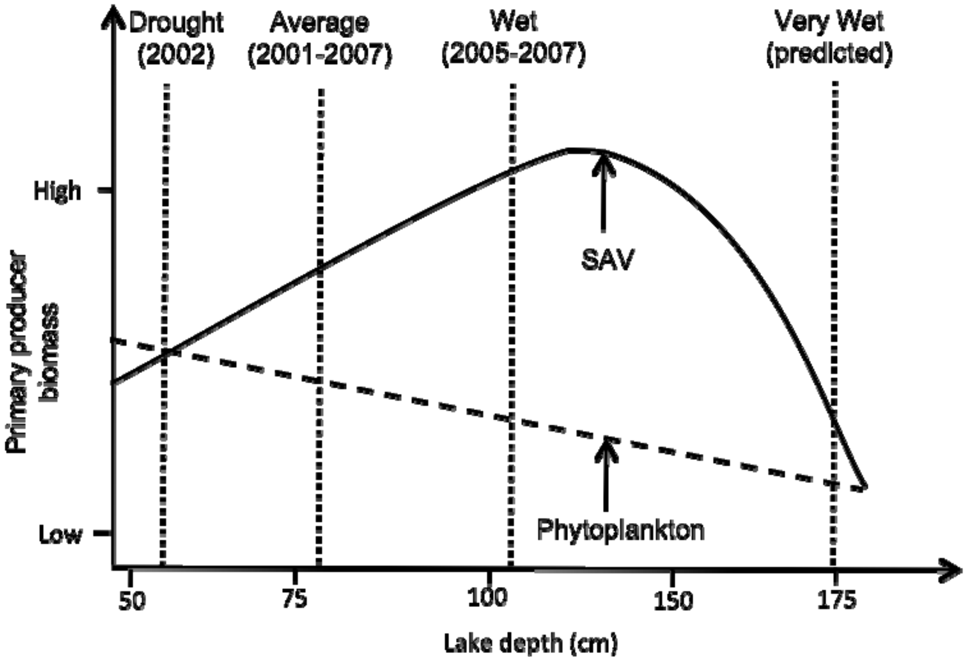


Figure 4-6. Conceptual model between lake depth and macrophyte cover (solid line) and phytoplankton biomass (dashed line) based on relative SAV cover and phytoplankton biomass during wet, dry and average years of precipitation (dotted lines), as well as SAV biomass along a water depth gradient in the study lakes. The predicted relative abundance during very wet years is also indicated.

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Chapter 5 - **General Discussion and Conclusions**

The theory of alternative stable states for shallow lakes was inspired by observations that lakes tended to shift abruptly between a clear and turbid state, and once a lake became turbid it was resistant to restoration efforts (Phillips et al. 1978; Scheffer et al. 1993). Alternative regimes in shallow lakes are typically persistent over time (Blindow et al. 1993; Scheffer et al. 1993; Hargeby et al. 2007). Research revealed that a number of internal feedback mechanisms maintained the clear and turbid states making them resistant to disturbance (Moss 1990; Scheffer et al. 1993; Jeppesen et al. 1997; Scheffer 1998).

This study investigated whether inter-annual fluctuations in precipitation may contribute to the frequent switches between alternative regimes in shallow lakes on the Boreal Plains. Furthermore, the internal positive feedback mechanisms that maintain the ecosystem states in other shallow lakes may be weak (i.e. the states lack resilience). I explored the effects of inter-annual changes in precipitation on regional lake dynamics (Chapter 4), within lake processes and lake and landscape features affecting persistence of the alternative regimes (Chapter 3), and the internal positive feedback mechanisms maintaining the alternative regimes (Chapter 2 & 3). Below I review the major findings of these studies and examine their significance to the field of shallow lake ecology.

Fluctuations in precipitation drive frequent alternative regime shifts

The original theory of alternative stable states in shallow lakes considered the effects of occasional disturbances (Scheffer et al. 1993). However, on the Boreal Plains fluctuations in annual precipitation are dramatic – the wettest year of the study was more than double the precipitation of the driest year. In this system disturbances appear to be the rule rather than the exception, and as such are likely to be far from equilibrium most of the time (Hastings 2004).

Alternative regime switches in shallow lakes on the Boreal Plains appear driven by fluctuations in annual precipitation that affect the physical and chemical lake conditions, in turn affecting the relative growth of macrophytes and phytoplankton. Low annual precipitation concentrated nutrients, phytoplankton biomass and organic matter in the water column, shading SAV and promoting a turbid, phytoplankton-rich regime (Figure 5-1a). During wet periods precipitation diluted nutrient concentrations and turbidity, decreasing phytoplankton biomass and promoting a clear water, SAV-rich regime (Figure 5-1b).

Lakes on the Boreal Plains are sensitive to fluctuations in inter-annual precipitation due to constraints imposed by the climate and landscape. The relatively flat topography, glacially derived sediments, and sub-humid climate produce low surface water runoff (Redding and Devito 2008). The lakes are small, shallow, and isolated, and the hydrologic budget is dominated by precipitation inputs (83 – 95%) and evaporative outputs (93 – 96%), with the remainder provided from lateral groundwater exchange with the surrounding peatlands (Ferone et al. 2004). Lake water on the Boreal Plains is nutrient-rich reflecting mesic peat and gyttja water sources from shallow groundwater inputs (Ferone et al. 2004), whereas precipitation is nutrient poor (Ferone 2001). Evaporative concentration of nutrients and organic matter in isolated lakes is an important mechanism influencing phytoplankton production, as seen in other boreal lakes (Schindler et al. 1996), in Lake Vortsjarv, a large shallow lake in Estonia (Noges et al. 1999) and several floodplain lakes (Sokal et al. 2008; Loverde-Oliveira et al. 2009; McGowan et al. 2011).

Macrophyte abundance was better predicted by lake depth rather than precipitation quantities. Macrophytes have relatively slow population dynamics compared to phytoplankton and their growth in a given year is a function of water clarity (dependent on water depth and turbidity) and SAV abundance from the previous year. During the study SAV cover increased with lake depth and was significantly higher in 2007 following three years of higher water levels. The SAV biomass – lake depth study indicates a unimodal relationship peaking at 125cm. SAV growth is presumably limited at shallower depths (< 125cm) by increased turbidity, and at deeper depths (> 125cm) by light attenuation due to increasing water depth. There was little SAV biomass beyond 175cm depth. The study period was relatively dry; average annual precipitation was 90 mm below the 30 year average. During this time lake depth averaged 83 cm, peaking in 2006 at 104 cm. If wetter conditions return, similar to the long-term average, deeper lakes (> 175 cm) will likely exhibit a clear regime with low phytoplankton biomass and low macrophyte coverage. Such a regime was observed in 12% of lakes in this study and deeper lakes in a large synoptic survey of the region (Bayley et al. 2003). Whether this regime is a unique alternative regimes (i.e. a 'stable' equilibrium point) or a non-equilibrium phase of the clear, SAV dominant regime is unclear.

Changes in water levels have been natural triggers for switches in SAV dominance in other studies on shallow lakes (Havens et al. 2004; Van Geest et al. 2007; Loverde-Oliveira et al. 2009). The response of SAV abundance to changes in lake depth depends on how it affects water clarity. Water level rises increased water clarity promoting a SAV-dominant regime in shallow floodplain lakes of the Pantanal River (Loverde-Oliveira et al. 2009), similar to lakes on the Boreal Plains. In contrast, water level decreases improved light conditions and promoted a transient SAV-rich regime in hypereutrophic shallow lakes on the Rhine River (Van Geest et al. 2007).

Only the clear, SAV-dominated regime exhibited persistence from year-to-year in shallow lakes on the Boreal Plains. SAV cover was temporally correlated with, and a significant predictor of SAV cover the following year. SAV abundance showed a significant increase only in 2007, following 3 years of high water levels. Additionally, a broader study of lakes in the region found that over a 20-year period, all the lakes that were stable (20%) were clear, and average lake TP concentrations in the region are typical of a clear water state (< 70 μg/L during most years) (Bayley et al. 2007). The perennial nature and relatively slow growth habit of many SAV species imparts resilience to the regime. The tendency for higher resilience of the clear state has been suggested in other studies of shallow lakes (Hargeby et al. 2007). In contrast, phytoplankton exhibited little "memory" from year-to-year. There were strong and frequent inter-annual shifts in phytoplankton biomass associated with fluctuating precipitation levels.

Vegetation appears better able to tolerate turbid conditions in shallower lakes. The high SAV and high phytoplankton regime were observed in the shallowest lakes in this study, as well as a broader synoptic survey of the region (Bayley et al. 2003). This regime is likely a non-equilibrium, transient phase of the clear, SAV-dominant regime. Vegetated lakes are likely to remain so because vegetation can be gained and lost gradually in the shallower and deeper parts of the lake (Amemiya et al. 2007), and plants are less affected by turbidity at shallower sites (van Nes et al. 2002). Studies have proposed that hysteresis may be less pronounced and even disappear if the depth profile of a lake is less flat (van Nes et al. 2002). These lakes are likely to revert to a clear, SAV-rich regime following high precipitation events.

Lake and landscape factors affecting the persistence of the alternative regimes

Alternative state theory tends to rely on simple models e.g. (Scheffer 1998) that ignore the spatial heterogeneity of real ecosystems (Scheffer et al. 2003). Spatial heterogeneity tends to cause the response of system to be localized. Averaged over the landscape, this results in gradual rather than sudden ecological change, and reduces the chance that large scale shifts between alternative regimes are found (van Nes et al. 2005). Few studies have examined relationships between spatial heterogeneity and lake dynamics (Magnuson et al. 1990; Webster et al. 2000).

I was interested in how spatial variability in lake features would affect the persistence of alternative regimes to regional changes in climate (the primary disturbance affecting the study region) over time. Shifts in alternative regimes do not happen at the same time, because different lakes have different local properties. I examined relationships between lake and landscape factors and the persistence of each alternative regime in each lake, which averaged the response of lakes to changes in precipitation during the study period.

The most important controls of the persistence of the SAV-rich and phytoplankton-rich regimes were lake-specific factors and within lake processes. The SAV-rich regime persistence increased in shallower lakes, with abundant predaceous macroinvertebrate predators, and low TP concentration. Higher persistence of the phytoplankton-rich regime was associated with higher *Daphnia* dominance, and higher TP concentration. However, landscape features may also explain some of the variation in the persistence of alternative regimes. Smaller lakes at lower elevations, with a higher proportion of wetlands in the local catchment tended to support a more persistence SAV-rich regime. The persistence of the phytoplankton-rich regime may be partially explained by lake size and lake connectivity with groundwater (Figure 3-10).

The persistence of the SAV-rich regime increased with in shallower lakes, increasing biomass of macroinvertebrate predators, and decreasing TP concentration. Deeper lakes (> 112 cm) were associated with the least persistent SAV-rich regime. Deeper lakes may limit SAV growth due to light limitation and negative trophic effects from fish. A SAV biomass – lake depth survey in the region found a unimodal relationship with SAV biomass peaking at 125 cm water depth (Chapter 4). SAV growth is presumably limited by light attenuation at deeper depths. Another factor associated with deeper lakes is an increased prevalence of planktivorous fish. Fish-bearing lakes had significantly higher maximum depth (153 cm versus 101 cm, $P < 0.0001$). Fish presence was two times lower in SAV-rich lakes compared to SAV-poor lakes. This suggests that fish, via top-down predatory effects on large zooplankton grazers, promote a turbid water state in these lakes, as previously observed in shallow lakes on the Boreal Plains (Norlin et al. 2005), and other shallow lake systems (Jeppesen et al. 1990; Hanson et al. 1994; Zimmer et al. 2001).

Large predatory macroinvertebrates are top predators in shallow fishless lakes where they are abundant and diverse compared to fish-bearing water bodies (Mallory et al. 1994; Batzer et al. 1996; Wellborn et al. 1996; Tonn et al. 2004; Hornung et al. 2006). The positive association between biomass of predaceous macroinvertebrates and the persistence of the SAV-rich regime suggests that predaceous macroinvertebrates play an important role in helping to maintain the SAV-rich regime. The macroinvertebrate community was largely ignored in the initial model of Scheffer et al. (1993). The SAV-rich regime was associated with a higher abundance of macroinvertebrates including predators (2X) and Gastropods (3X), and lower periphyton biomass. Grazing macroinvertebrates and zooplankton likely suppress epiphyton that would otherwise shade SAV.

Low TP concentration ($> 58\ \mu g\ L^{-1}$) was associated with a more persistent SAV-rich regime. Eutrophication is known to promote phytoplankton biomass, increase turbidity and suppress SAV coverage (Jeppesen et al. 1998; Scheffer 1998). Phosphorus is the limiting nutrient in these lakes and previous studies have found that switches in lake regimes were related to TP concentration (Bayley et al. 2007).

Lakes with high *Daphnia* dominance and high TP concentration were associated with a more persistent phytoplankton-rich regime. High TP was associated with a more persistent phytoplankton-rich regime, as has been previously demonstrated in shallow lakes on the Boreal Plains (Bayley et al. 2007) and other shallow lake systems (Scheffer et al. 1993). I suspect that the association between a higher dominance of *Daphnia* and increased persistence of the phytoplankton-rich regime is a consequence of bottom-up processes rather than top-down controls. None of the lakes associated with high *Daphnia* dominance were fish-bearing. Higher *Daphnia* dominance has been associated with higher levels of resource abundance (Romanovsky et al. 1985). This may be due to a superior ability to access a broader size spectrum of algae compared to many small-bodied zooplankton (Burns 1968; Neill 1975; DeMott 1995). *Daphnia* have higher phosphorus requirements compared to many small-bodied Cladocera and copepods, and may be favoured when algal C:P and N:P ratios are low (Sterner et al. 1994; Urabe et al. 1997; DeMott 1998; Steiner et al. 2003).

I hypothesized that the persistence of alternative regimes to inter-annual changes in precipitation would depend on a lake's relative sensitivity to drought. The SAV-rich regime would be more persistent in lakes that were resistant to drought, whereas the phytoplankton-rich regime would be more persistent in lakes that were more sensitive to drought. Lake sensitivity to drought was predicting to increase with decreasing lake size and maximum depth (Wolfe et al. 2007), increasing elevation in the landscape (Webster et al. 2000), decreasing groundwater connectivity (Kratz et al. 1997), and decreasing shallow ground water connection with adjacent peatlands (Ferone et al. 2004). Finally, the heterogeneity of surficial geology types (glaciofluvial > morainal > organic) may affect a lake's sensitivity to drought through the integration of landscape features such as lake position, extent of wetlands in the buffer, and/ or lake morphometry.

The persistence of the SAV-rich regime was reasonably well modelled by landscape factors (pseudo $R^2 = 0.59$ versus 0.66 for lake-specific factors). In contrast, the persistence of the phytoplankton-rich regime was poorly modelled by landscape factors (pseudo $R^2 = 0.19$ versus 0.50 for lake-specific factors).

Smaller lakes promoted the persistence of both phytoplankton-rich and SAV-rich regimes, although I propose that lake size affected the persistence of the primary producer communities differently. Smaller lakes likely promoted the phytoplankton-rich regime through increased susceptibility to evaporative concentration during drought, which has been associated with increased phytoplankton biomass in shallow lakes on the Boreal Plains (Chapter 4). The persistence of the SAV-rich regime was likely higher in smaller lakes due a variety of mechanisms. Although the mechanisms cannot be resolved here, the positive effect of lake size on the stability of a SAV-dominated state in these lakes may be associated with wind effects, colonization time, nitrogen retention time and fish effects. Other studies have similarly found that smaller lakes tend to remain in a vegetated state longer and may tend to be systematically closer to a vegetated stable state (Jeppesen et al. 1990; Van Geest et al. 2003; Sondergaard et al. 2005; Scheffer et al. 2006; Van Geest et al. 2007).

Contrary to our hypothesis, increased wetland area in the local catchment decreased the persistence of the SAV-rich regime. The wetlands are likely functioning primarily as a source of phosphorus to lakes, which is eclipsing their role as an attenuator of droughts. Wetland extent in a lake's catchment has been correlated with increased lake TP in shallow lakes on the Boreal Plains (Devito et al. 2000). A process-based hydrology study found surface hydrologic connections to wetlands were the dominant source of phosphorus to the annual P budget of two shallow lakes on the Boreal Plains (Ferone 2001).

Lakes lower in elevation tended to support a more persistent SAV-rich regime consistent with my hypothesis. I presume that effects of drought are attenuated in lowland lakes due to increased hydrologic inputs from upstream sources, such as shallow groundwater pathways from local peatlands. Similar patterns were observed in shallow lakes on the Boreal Plains in response to logging. Recharge lakes, located higher in the flow system, showed higher TP responses to logging activity in their catchments compared to lower elevation flow-through lakes (Devito et al. 2000; Ferone et al. 2004). Similar spatial patterns in response to drought were observed in a groundwater-dominated system of glacial origin in northern Wisconsin (Webster et al. 2000). During drought, as local flow paths reverse or diminish, groundwater from more stable regional flow paths is thought to provide a larger proportion of the water input to lowland lakes.

Lakes with higher Ca + Mg tended to support a more persistent phytoplankton-rich regime. This was contrary to my prediction that increased groundwater connectivity would decrease the sensitivity of a lake to fluctuations in precipitation and hence decrease the persistence of the phytoplankton-rich regime. Lakes with higher Ca + Mg tended to occur on organic deposits located lower in the regional district, and tended to have a high proportion of wetland in the local catchment. Lakes with higher Ca + Mg showed less inter-annual variability in phosphorus levels in different lakes on the Boreal Plains (Devito et al. 2000). This suggests that the more persistent phytoplankton-rich regime may be maintained by groundwater flow paths that minimize changes in phosphorus.

Internal positive feedback mechanisms maintaining the resilience of alternative regimes

Switches between alternative regimes are often induced by an external disturbance, such as weather changes, but the persistence of each regime is stabilized by internal positive feedback mechanisms (Moss 1990; Scheffer et al. 1993). The rapid and repeated regime shifts observed in shallow lakes on the Boreal Plains (Bayley et al. 2007) suggests that internal mechanisms that provide internal resistance to external changes are weak or lacking. Top-down effects mediated by fish played a central role in maintaining alternative regimes in the initial model of Scheffer et al. (1993). However, the majority of shallow lakes in the Boreal Plains are fishless due to the harsh winter conditions which result in fish kills (Conlon 2002; Tonn et al. 2004). In the absence of fish, macroinvertebrate predators may play an important role in structuring the food web. Macroinvertebrate predators have been shown to cause day-night migration of zooplankton, reduced zooplankton abundance, and alter zooplankton community structure, including reduced dominance of *Daphnia* (Gilbert et al. 2001; Shurin 2001; Steiner et al. 2003). Few studies have examined the importance of macroinvertebrates in maintaining alternative regimes in fishless shallow lakes.

I hypothesized that the SAV-rich regime would be associated with a community that was fishless, with abundant and rich macroinvertebrates, and an abundant Cladocera community with high *Daphnia* dominance. Macroinvertebrate and zooplankton grazers would play an important role in suppressing epiphyton and phytoplankton and promoting a SAV-rich regime. In contrast, the phytoplankton-rich regime would be associated with a community dominated by plantivorous fish, small cladocerans and increased phytoplankton biomass, consistent with the initial model of Scheffer et al. (1993).

Zooplankton appear to play an important role in suppressing phytoplankton in SAV-rich lakes: the ratio of cladocerans/ chl-*a*, an index of microcrustacean herbivory on phytoplankton was two times higher in SAV-rich lakes than SAV-poor lakes. Additionally, over 70% of the zooplankton community was composed of cladocerans that graze on phytoplankton in SAV-rich lakes, compared to 57% in SAV-poor lakes. The high proportion of cladocerans is typical of lakes with low fish predation pressure on zooplankton (Jeppesen et al. 2000; Zimmer et al. 2002). Cladocera dominance of the zooplankton community was high compared to lakes in southern Alberta (47%) and Denmark (47%) (Jackson et al. 2007).

Macroinvertebrates in fishless lakes appear to play an important role in suppressing periphyton biomass that would otherwise shade SAV. SAV-rich regimes were associated with higher abundance of macroinvertebrates including predators (2X) and Gastropods (3X), a higher abundance of zooplankton grazers known to feed on periphyton, and lower periphyton biomass (3X). Grazing macroinvertebrates and zooplankton likely suppress epiphyton that would otherwise shade SAV. Field evidence suggests that periphyton biomass is primarily constrained by grazers rather than nutrients ((Jones et al. 2002; Jones et al. 2003; McIntyre et al. 2006), and see Hillebrand (2002) for a review). A previous study found a fish – macroinvertebrate grazer – periphyton trophic cascade associated with SAV-dominated lakes (Jones et al. 2003). Mesocosm experiments found a predaceous macroinvertebrate precipitated a benthic trophic cascade whereby *Dytiscus alaskanus* reduced the biomass of algivorous snails and other herbivores leading to increased production of periphyton (Figure 5-3). This study suggests that macroinvertebrate grazers may also play an important role in suppressing periphyton biomass and promoting a SAV-dominant regime in fishless shallow lakes.

SAV-rich lakes were associated with a higher biodiversity of macroinvertebrate species. The insurance value of biodiversity may be significant in increasing the resilience of the SAV-rich regime in the face of disturbance. Variability in responses of species within functional groups to environmental change is critical to ecosystem resilience (Chapin et al. 1997; Norberg et al. 2001).

According to trophic cascade theory, complex, diverse food webs would be expected to have dissipated trophic effects (Strong 1992). However, other attributes of fishless lake communities are predicted to be vulnerable to trophic cascades: the conditions are mesotrophic with periphytic algae at the base of the food web that is vulnerable to herbivory (Strong 1992). The macroinvertebrate communities appeared to have similar predaceous effects on lower trophic levels in the field survey and mesocosm experiment, thus trophic effects were strong despite the high species richness. Gastropods and other grazers consumed periphyton. The macroinvertebrate predator community suppressed small and large species of Cladocera, leading to a trophic level effect. This study provides further evidence that trophic interactions can be important in structuring freshwater littoral food webs despite their high diversity (Brönmark 1994; Brönmark et al. 1997; Nystrom et al. 2001; Jones et al. 2003).

Top-down processes appear weak or absent in the phytoplankton-rich regime, which may contribute to their low persistence. Food web effects on phytoplankton appear weak: edible algae were abundant, the chlorophyll-*a* per unit TP was significantly higher, the cladoceran/ chl-*a* ratios were significantly lower, and the prevalence of fish were similar in phytoplankton-rich and phytoplankton-poor lakes. I suspect that inter-specific competition and bottom-up resource-based effects control the zooplankton community structure. *Daphnia* constituted a larger proportion of the Cladocera population in phytoplankton-rich lakes (47%) compared to phytoplankton-poor lakes (35%). *Daphnia* dominance is favoured at higher levels of resource abundance (Romanovsky et al. 1985) and when larger-sized resources predominate as they can access a broader size spectrum and large size classes of algae compared to many small-bodied zooplankton (Burns 1968; Neill 1975; DeMott 1995). Additionally, *Daphnia* have high phosphorus requirements and often dominate when algal C:P and N:P ratios are low (Sterner et al. 1994; Urabe et al. 1997; DeMott 1998; Steiner et al. 2003).

Future research

This study identified some landscape attributes that may be structuring the response of shallow lakes on the Boreal Plains to inter-annual variations in precipitation, including lake morphometry, elevation, connectivity with groundwater, and the proportion of wetlands in the local catchment. Although surficial geology classes where not identified as a primary factor structuring patterns in the persistence of alternative regimes, patterns in lake elevation, size, and groundwater connectivity may be present. The study lakes were predominately small and isolated, in the upper catchment of the Peace watershed, with little variation in landscape position.

The concept of lake landscape position provides a general framework to explicitly investigate spatial patterning in lake conditions and to identify mechanisms driving variation in ecological process and dynamics in lakes. Landscape position of a lake is a combination of the hydrologic description, including measures of surface water and groundwater connectivity, with information on the spatial placement of the lake (Kratz et al. 1997). Future research should investigate what patterns of lake response variables (e.g.

nutrients, solutes, acid rain sensitivity, drought sensitivity) are related to landscape position by targeting lakes along a wider gradient of landscape position. Lake landscape position is likely related to lake morphometry and local catchment features due to geomorphological constraints associated with landscape position (Kratz et al. 2005). The development of a conceptual hierarchical framework that incorporates these relationships and their relative importance may help suggest underlying mechanisms driving variability in lakes in seemingly similar settings.

Figures

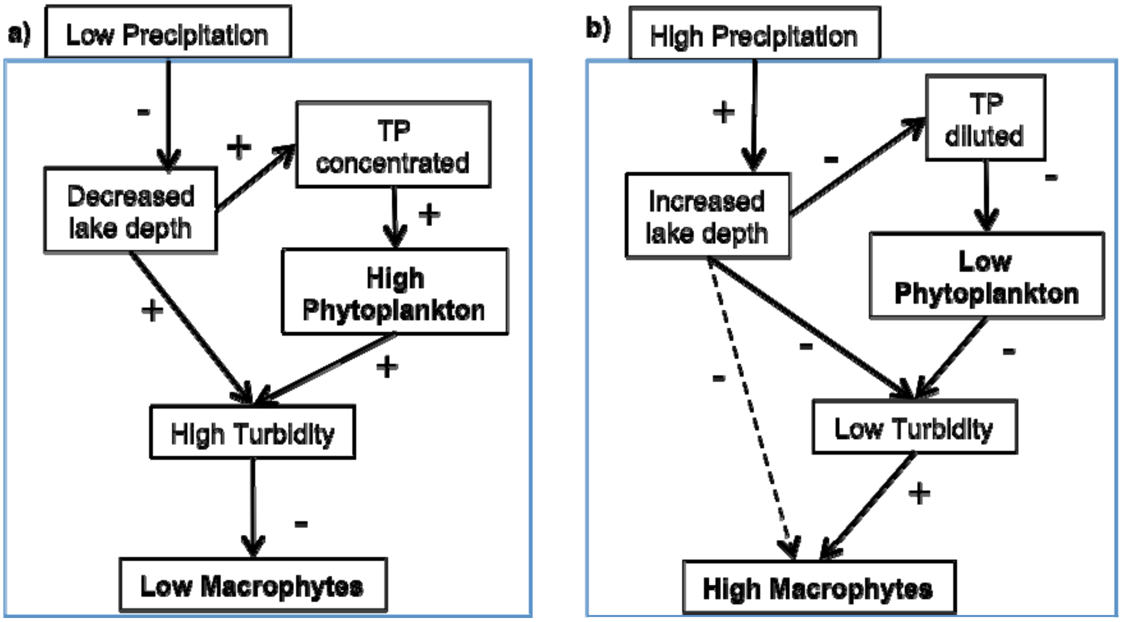

Figure 5-1. Conceptual model whereby a) low precipitation promotes a turbid, high phytoplankton regime, and b) high precipitation promotes a clear, high macrophyte regime. The dashed line indicates the predicted negative effects of water depth on macrophytes abundance in very wet years (i.e. water depth > 175 cm).

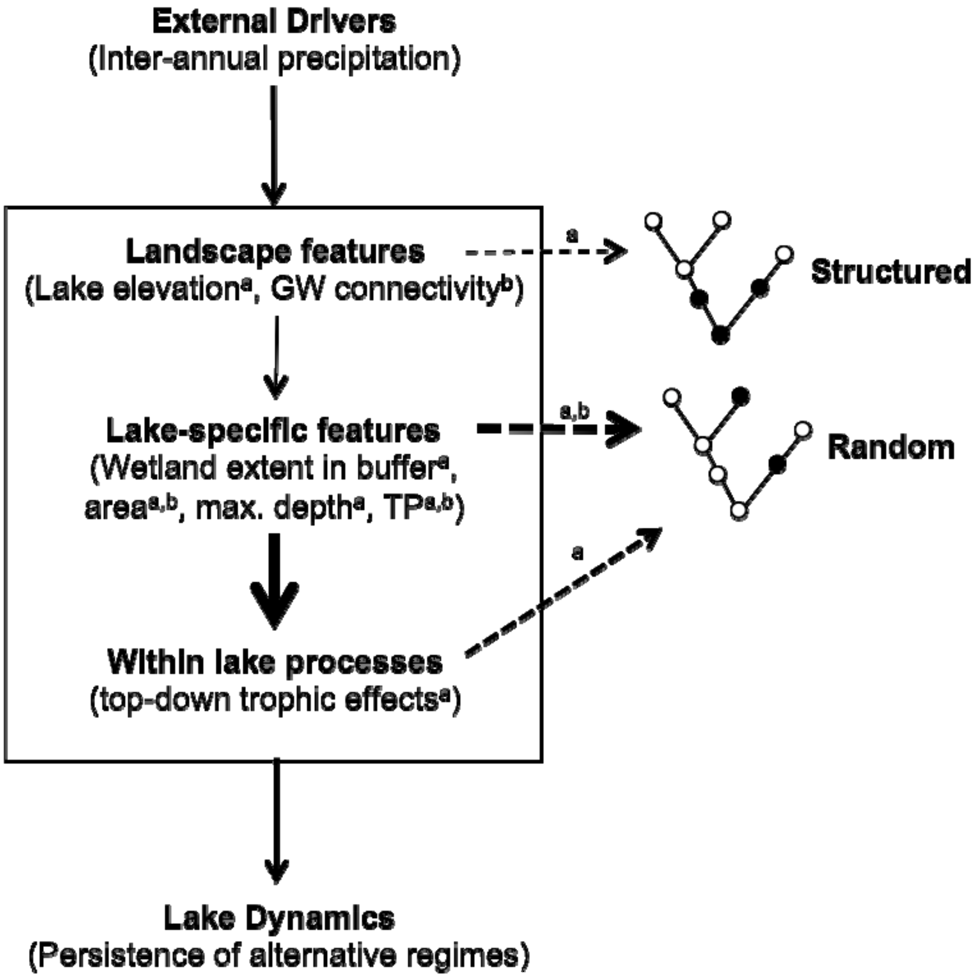

Figure 5-2. Diagram of hierarchy of controls on the persistence of alternative regimes and spatial patterns in lake dynamics generated at each level of control (modified from (Kratz et al. 2005). Strongest control resides at the lake-specific level which results in the persistence of alternative regimes exhibiting a predominately random spatial pattern. The weight of the arrows indicates the relative strength of the controls. [a] and [b] indicates effects on the persistence of the SAV-rich regime and phytoplankton-rich regime, respectively.

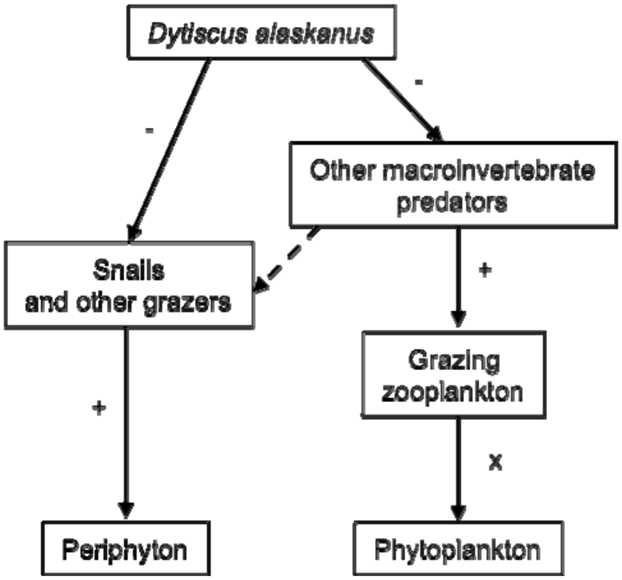

Figure 5-3. Diagram of trophic interactions observed in fishless boreal pond communities. Dytiscid predation of snails and other grazers led to increased periphyton; other predatory macroinvertebrates likely facilitated the consumption of the herbivores (dashed line). Dytiscid consumption of other predatory macroinvertebrates led to increased abundance of zooplankton. No top-down effects of dytiscids were detected for phytoplankton abundance. + or – indicates whether the interaction is positive or negative and the x indicates no effect (Cobbaert et al. 2010).

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Appendix A. Zooplankton taxa and biomass.

Taxa	**Authority**	**Sum of biomass (µg L^{-1})**
Acroperus harpae	(Baird, 1834)	14.21
Alona affinis	Leydig, 1860	8.27
Alona costata	G. O. Sars, 1862	47.56
Alona guttata	G. O. Sars, 1862	353.48
Alona quadrangularis	(O. F. Müller, 1776)	0.31
Alona rectangula	Sars, 1861	0.62
Alona sp.		4.69
Alonella excisa	(Fischer, 1854)	0.62
Benthic cladocerans		25.28
Bosmina longirostris	(O. F. Müller, 1776)	3984.31
Calanoid copedites I-V		2262.80
Camptocerus rectirostris	Schoedler, 1862	341.98
Ceriodaphnia quadrangula	(O. F. Müller, 1785)	24098.90
Chydoridae other		883.05
Chydorus sphaericus	(O. F. Mueller, 1785)	25461.88
Copepod Nauplii		914.66
Cyclopoid adults		2849.54
Cyclopoid copedites I-V		8937.88
Daphnia rosea (form *dentifera)*	G. O. Sars, 1862	34450.13
Daphnia pulex	Leydig, 1860	9192.69
Daphnia sp.		12172.16
Diacyclops thomasi	(S. A. Forbes, 1882)	1027.48
Diaphanosoma birgei	Korinek, 1981	2843.72
Diaptomus siciloides	Lilljeborg, 1889	13626.98
Eucyclops agilis	(Koch, 1838)	4484.50
Eurycercus lamellatus	(O. F. Mueller, 1776)	24.62
Eurycercus sp.		46.28
Graptoleberis testudinaria	(Fischer, 1848)	1034.32
Harpacticoida		55.13
Ilyocryptus sordidus	(Liévin, 1848)	3.08
Juvenile Cladoceran		2070.58
Leydigia sp.		1.00
Macrocyclops albidus	(Jurine, 1820)	8845.78
Macrothricidae		15.48
Mesocyclops leukarti	(Claus, 1857)	8.84
Microcyclops rubellus	(Lilljeborg, 1901)	261.30
Ostracoda		24521.52
Paracyclops poppei	(Rehberg, 1880)	130.18
Pleuroxus denticulatus	(Birge, 1879)	74.28
Pleuroxus procurvus	Birge, 1879	330.51
Pleuroxus sp.		374.93
Pleuroxus trigonellus	(O. F. Müller, 1776)	9.22
Polyphemus pediculus	(Linnaeus, 1761)	1166.78
Scapholeberis kingi	G. O. Sars, 1888	80.69
Simocephalus vetulus	(O. F. Müller, 1776)	10624.23
Skistodiaptomus oregonensis	(Lilljeborg in Guerne and Richard, 1889)	11173.43

Appendix B. Macroinvertebrate taxa, feeding guild and biomass.

Taxa	Authority	Major taxonomic group	Feeding guild [a]	Sum of biomass (µg L^{-1})
Acarina (deutonymph)		Arachnida	Predator	5.68
Aeshna		Anisoptera	Predator	843.03
Agabus	Leach, 1817	Coleoptera	Predator	198.60
Agrayela		Trichoptera	G/C	73.85
Alboglossiphonia heteroclita	(Linnaeus, 1761)	Hirudinea	Predator	474.57
Amiocentrus		Trichoptera	G/C	0.51
Amnicola limosus	(Say, 1817)	Gastropoda	Scraper	205.11
Anagapetus		Trichoptera	Scraper	4.07
Analetris	Edmunds, 1972	Ephemeroptera	G/C	48.92
Anax	Leach, 1815	Anisoptera	Predator	678.83
Anisoptera		Anisoptera	Predator	3.95
Aphididae		Hemiptera	Predator	2.63
Arachnida		Arachnida	Predator	63.88
Argia	Rambur, 1842	Zyoptera	Predator	0.09
Arrenurus	Duges, 1835	Arachnida	Predator	222.71
Baetidae		Ephemeroptera	G/C	299.68
Bakerilymnaea		Gastropoda	Scraper	109.96
Brychius	Thomson, 1859	Coleoptera	Scraper	33.20
Caenis	Stephens, 1835	Ephemeroptera	G/C	609.21
Callibaetis	Eaton, 1881	Ephemeroptera	G/C	0.68
Centroptilum	Eaton, 1869	Ephemeroptera	G/C	3.37
Ceratopogonidae		Ceratopogonidae	Predator	2801.73
Chaoborus	Lichtenstein, 1800	Chaoboridae	Predator	4059.17
Chironomidae		Chironomidae	G/C	4762.38
Chrysomelidae		Coleoptera	Shredder	269.19
Chrysops		Diptera	Predator	0.78
Cicadellidae	Latreille, 1802	Hemiptera	Predator	13.41
Cloeon	Leach, 1815	Ephemeroptera	G/C	20.03
Coenagrion	Kirby, 1890	Zyoptera	Predator	4944.88
Coenagrionidae		Zyoptera	Predator	518.88
Coleoptera		Coleoptera	Predator	1.40
Collembola		Collembola	G/C	0.65
Colymbetes	Clairville, 1806	Coleoptera	Predator	9.88
Cordulegastridae		Anisoptera	Predator	10.77
Cordulia shurtleffi	Scudder, 1866	Anisoptera	Predator	3362.99
Corisella	Lundblad, 1928	Hemiptera	Predator	42.26
Corixidae	Leach, 1815	Hemiptera	Predator	4764.41
Cristatella mucedo	Cuvier, 1798	Bryozoan	F/C	92.01
Culicidae		Diptera	F/C	50.02
Curculionidae	Latreille, 1802	Coleoptera	Shredder	76.91
Cymatia americana	Hussey, 1920	Hemiptera	Predator	776.57
Dasycorixa	Hungerford, 1948	Hemiptera	Predator	90.34
Desmopachria	Babington, 1841	Coleoptera	Predator	410.40

Desserobdella picta	(Verrill, 1872)	Hirudinea	Predator	331.24
Dina or Mooreobdella	R. Blanchard, 1892	Hirudinea	Predator	1594.32
Diptera		Diptera	G/C	203.03
Diura	Billberg, 1820	Plecoptera	Scraper	4.01
Dolomedes		Arachnida	Predator	130.59
Donacia	Fabricius, 1775	Coleoptera	Shredder	1.48
Dytiscidae	Leach, 1815	Coleoptera	Predator	1613.01
Dytiscus	Linnaeus, 1758	Coleoptera	Predator	12605.37
Ecclisomyia		Trichoptera	G/C	1.76
Empididae		Diptera	Predator	0.40
Enallagma	Charpentier, 1840	Zyoptera	Predator	439.42
Ephemeroptera		Ephemeroptera	G/C	30.19
Epitheca	Burmeister, 1839	Anisoptera	Predator	263.88
Erpobdella punctata	(Leidy, 1870)	Hirudinea	Predator	5672.53
Erpobdellidae		Hirudinea	Predator	1439.84
Eylais	Latreille, 1796	Arachnida	Predator	255.60
Fabria		Trichoptera	Shredder	115.06
Frontipoda	Koenike, 1891	Arachnida	Predator	3.03
Gammarus lacustris	G. O. Sars, 1863	Amphipoda	Shredder	22656.69
Gastropoda		Gastropoda	Scraper	259.08
Gerris	Fabricius, 1794	Hemiptera	Predator	105.13
Glossiphonia complanata	(Linnaeus)	Hirudinea	Predator	4147.50
Glossiphoniidae	Vaillant, 1890	Hirudinea	Predator	106.38
Glossosoma		Trichoptera	Scraper	1.39
Graphoderus	Dejean, 1833	Coleoptera	Predator	894.50
Gyraulus	Agassiz, 1837	Gastropoda	Scraper	699.38
Gyraulus crista	(Linnaeus, 1758)	Gastropoda	Scraper	460.87
Gyrinus	Geoffroy, 1762	Coleoptera	Predator	45.22
Haliplidae	Aubé, 1836	Coleoptera	Shredder	29.05
Haliplus	Latreille, 1802	Coleoptera	Shredder	1019.40
Helisoma	Swainson, 1840	Gastropoda	Scraper	78009.04
Helobdella elongata	(Castle, 1900)	Hirudinea	Predator	2.29
Helobdella stagnalis	(Linneaus)	Hirudinea	Predator	729.44
Hemiptera		Hemiptera	Predator	143.14
Hesperocorixa	Kirkaldy, 1908	Hemiptera	Shredder	175.39
Hirudinea		Hirudinea	Predator	451.23
Hyallela azteca	Saussure, 1858	Amphipoda	G/C	105975.92
Hydaticus	Leach, 1817	Coleoptera	Predator	3.17
Hydra	Linnaeus, 1758	Cnidaria	Predator	119.43
Hydrachna	Fabricius, 1801	Arachnida	Predator	7.81
Hydrachnidia		Arachnida	Predator	26.26
Hydrodroma	Koch, 1837	Arachnida	Predator	8.56
Hydroptilidae		Trichoptera	Shredder	13.45
Hydrozetes	Berlese, 1902	Arachnida	Predator	11.79
Hygrotus and Hydroporus	Stephens, 1828	Coleoptera	Predator	2849.48
Hymenoptera		Hymenoptera	Predator	82.76
Ilybius	Erichson, 1832	Coleoptera	Predator	538.72

Ischnura	Charpentier, 1840	Zyoptera	Predator	1.56
Laccophilus	Leach, 1815	Coleoptera	Predator	71.93
Lepidostoma		Trichoptera	Shredder	0.52
Lepidostomatidae		Trichoptera	Shredder	51.53
Lestes	Leach, 181	Zyoptera	Predator	472.42
Leucorrhinia	Brittinger, 1850	Anisoptera	Predator	3139.19
Libellula	Linnaeus, 1758	Anisoptera	Predator	1853.50
Limnephilidae		Trichoptera	Shredder	139.60
Limnephilus		Trichoptera	Shredder	3.33
Limnesia	Koch, 1835	Arachnida	Predator	171.33
Limnochares	Latreille, 1796	Arachnida	Predator	1.30
Limnoporus	Stål, 1868	Hemiptera	Predator	15.95
Liodessus	Guignot, 1939	Coleoptera	Predator	323.39
Lymnaea stagnicola	(Linnaeus)	Gastropoda	Scraper	38599.51
Lymnaeidae		Gastropoda	Scraper	23.78
Mayatrichia		Trichoptera	Scraper	2.75
Melyridae	Leach, 1815	Coleoptera	Predator	1.21
Menetus opercularis	(Gould, 1847)	Gastropoda	Scraper	709.47
Mesovelia mulsanti	White, 1879	Hemiptera	Predator	71.85
Mesoveliidae	Douglas and Scott, 1867	Hemiptera	Predator	73.77
Microvelia	Westwood, 1834	Hemiptera	Predator	0.14
Midea	Bruzelius, 1854	Arachnida	Predator	0.12
Mideopsis	Neuman, 1880	Arachnida	Predator	552.06
Mystacides		Trichoptera	Predator	0.19
Nehalennia	Selys, 1850	Zyoptera	Predator	8.90
Nemata		Nematoda	F/C	6.75
Nephelopsis obscura	(Verrill)	Hirudinea	Predator	34306.93
Neumania		Arachnida	Predator	5.23
Noctuidae		Lepidoptera	Shredder	86.53
Notonectidae		Hemiptera	Predator	3109.94
Oecetis		Trichoptera	Predator	37.55
Oligochaeta		Annelida	G/C	113.65
Orthocladiinae		Diptera	G/C	68.48
Orthotrichia		Trichoptera	Shredder	7.52
Oxidae		Arachnida	Predator	0.53
Oxyethira		Trichoptera	G/C	7.80
Parapsyche		Trichoptera	G/C	2.19
Pelecypoda		Bivalvia	F/C	15.18
Peltodytes	Regimbart, 1878	Coleoptera	Predator	34.89
Phryganea		Trichoptera	Shredder	226.47
Phryganeidae		Trichoptera	Shredder	74.11
Physa	Draparnaud, 1801	Gastropoda	Scraper	20039.78
Physidae		Gastropoda	Scraper	23.08
Piona		Arachnida	Predator	114.50
Pirata		Arachnida	Predator	0.61
Pisidiidae		Bivalvia	F/C	6043.77
Placobdella ornata	(Verrill, 1872)	Hirudinea	Predator	2326.09
Placobdella papillifera	(Verrill, 1872)	Hirudinea	Predator	123.27

Placobdella parasitica	(Say)	Hirudinea	Predator	47.90
Planorbidae		Gastropoda	Scraper	5095.70
Planorbula campestris	(Dawson, 1875)	Gastropoda	Scraper	4872.10
Plecoptera		Plecoptera	Predator	0.16
Podura aquatica	Linnaeus, 1758	Collembola	G/C	0.45
Probythinella lacustris	(F. C. Baker, 1928)	Gastropoda	Scraper	145.99
Promenetus	F. C. Baker, 1935	Gastropoda	Scraper	3646.32
Promenetus exacuous	(Say, 1821)	Gastropoda	Scraper	183.47
Promenetus umbilicatellus	(Cockerell, 1887)	Gastropoda	Scraper	7034.34
Psectrotanypus		Diptera	Predator	0.75
Ptilostomis		Trichoptera	Shredder	429.60
Pycnopsyche		Trichoptera	Shredder	0.16
Pyrrhalta	Joannis, 1865	Coleoptera	Shredder	6.44
Saldidae	Amyot and Serville, 1843	Hemiptera	Predator	66.34
Sciomyzidae		Diptera	Predator	5.44
Serratella	Edmunds, 1959	Ephemeroptera	G/C	0.11
Sialis	Latreille, 1802	Megaloptera	Predator	15.74
Sigara	Fabricius, 1775	Hemiptera	G/C	5048.48
Simuliidae		Diptera	F/C	0.35
Siphlonurus	Eaton, 1868	Ephemeroptera	G/C	412.97
Somatochlora	Selys, 1871	Anisoptera	Predator	5190.30
Stagnicola	Leach, 1830	Gastropoda	Scraper	5263.40
Staphylinidae		Coleoptera	Predator	163.22
Stylaria lacustris	(Linnaeus, 1767)	Annelida	G/C	47.41
Sympetrum	Newman, 1833	Anisoptera	Predator	424.32
Tanypodinae		Diptera	Predator	126.24
Theromyzon maculosum	(Rathe, 1862)	Hirudinea	Predator	1637.71
Tipulidae		Diptera	Shredder	33.93
Triaenodes		Trichoptera	Shredder	41.52
Trichoptera		Trichoptera	Predator	15567.87
Unionicola	Halderman, 1842	Arachnida	Predator	2.98
Valuata sincera ssp helicodea	Say, 1824	Gastropoda	Scraper	987.65
Valvata sincera sincera	Say, 1824	Gastropoda	Scraper	371.55
Veliidae		Hemiptera	Predator	0.59

[a] G/C = Gatherers/ Collectors; F/C = Filterers/ Collectors.

[b] M & C 1996 = Merritt and Cummins 1996; Barbour 1996 = Barbour et al. 1996.

Appendix C. SAV-rich versus SAV-poor lakes: differences in limnological variables and biological communities.

Mean and standard deviation for physical, chemical and biological variables in SAV-rich and SAV-poor lakes from surveys in August 2001-2007. P-values are from t-tests, Mann-Whitney U tests, or Chi-squared tests as appropriate. * indicates statistical significance at $\alpha = 0.05$, ** indicates statistical significance after a Bonferroni adjustment of $\alpha = 0.05/72 = 0.0007$.

	Units	n	Distribution	SAV-rich	SAV-poor	P value	Sign.
Abiotic variables							
Average depth	cm	156	Log normal	83 ± 34	83 ± 38	0.559	
Maximum depth	cm	120	Log normal	103 ± 42	120 ± 53	0.128	
Secchi depth	cm	152	Other	78 ± 30	70 ± 31	0.147	
Secchi depth: maximum depth	%	152	Other	91 ± 15	84 ± 24	0.049	*
Turbidity	NTU	132	Other	3.6 ± 4.4	6.3 ± 8.8	0.012	*
pH	pH units	153	Normal	8.4 ± 1.2	8.1 ± 1.1	0.152	
Electrical conductivity	µS cm^{-1}	153	Other	149.2 ± 78.0	146.7 ± 99.6	0.996	
Dissolved oxygen	mg l^{-1}	126	Other	9.2 ± 2.6	8.8 ± 2.8	0.320	
Total dissolved solids	mg l^{-1}	111	Other	0.10 ± 0.04	0.10 ± 0.04	0.199	
Dissolved organic carbon	mg l^{-1}	130	Other	64.4 ± 95.2	73.8 ± 106.2	0.876	
Alkalinity	mg l^{-1}	153	Log normal	68.8 ± 32.8	74.2 ± 31.7	0.410	
Bicarbonate	mg l^{-1}	153	Log normal	74.6 ± 39.3	81.7 ± 38.2	0.333	
Total phosphorus	µg l^{-1}	154	Other	79.4 ± 87.7	113.6 ± 123.6	0.082	
Total nitrogen	µg l^{-1}	156	Other	2298 ± 1556	3003 ± 2059	0.012	*
TN:TP (mass)	Ratio	154	Other	16.9 ± 8.1	18.0 ± 13.3	0.609	
Total dissolved phosphorus	µg l^{-1}	156	Other	35.7 ± 29.3	41.8 ± 63.8	0.209	
Soluble reactive phosphorus	µg l^{-1}	130	Other	8.2 ± 11.4	20.1 ± 61.0	0.927	
Total dissolved nitrogen	µg l^{-1}	130	Other	1633 ± 748	1867 ± 1064	0.237	
Ammonium	µg l^{-1}	156	Other	73 ± 368	150 ± 346	0.184	
Nitrate – Nitrite	µg l^{-1}	153	Other	7.8 ± 14.2	12.8 ± 26.1	0.184	
(NH_4^+ + NO_3^-): SRP	Ratio	133	Other	21.9 ± 80.4	49.5 ± 112.0	0.279	
Chloride	mg l^{-1}	87	Other	2.3 ± 4.0	1.6 ± 3.3	0.425	
Sulphate	mg l^{-1}	86	Other	9.4 ± 11.1	11.4 ± 14.6	0.707	
Sodium	mg l^{-1}	89	Other	2.4 ± 2.0	3.4 ± 3.9	0.093	
Potassium	mg l^{-1}	89	Log normal	3.6 ± 3.2	4.5 ± 3.4	0.131	
Calcium	mg l^{-1}	89	Normal	23.4 ± 11.6	24.9 ± 11.9	0.555	
Magnesium	mg l^{-1}	89	Other	7.0 ± 3.8	7.5 ± 3.6	0.351	
Iron	mg l^{-1}	75	Other	0.12 ± 0.12	0.10 ± 0.13	0.392	
Silica	mg l^{-1}	124	Other	1.6 ± 2.1	2.5 ± 2.1	0.005	*

Primary producers											
SAV abundance	Rating	156	Other	3.9	±	0.7	2.0	±	0.6	<0.0001	**
SAV abundance	% PVI	18	Normal	54	±	28	21	±	27	0.035	*
SAV biomass	g m^{-2}	86	Log normal	72	±	49	26	±	24	<0.0001	**
Periphyton biomass (Chl-*a*)	µg m^{-2}	23	Log normal	1,686	±	1,861	4,083	±	5,103	0.537	
Periphyton biomass (Fucoxanthin)	µg m^{-3}	23	Other	221	±	465	2,066	±	2,444	0.030	*
Periphyton biomass (Lutein)	µg m^{-4}	23	Other	441	±	463	558	±	691	0.930	
Periphyton biomass (Chl-b)	µg m^{-5}	23	Other	249	±	313	511	±	498	0.105	
Periphyton biomass (Violaxanthin)	µg m^{-6}	23	Other	71	±	172	0	±	0	0.022	*
Periphyton biomass (total)	µg m^{-7}	23	Log normal	2,669	±	2,748	7,218	±	8,020	0.390	
Phytoplankton biomass (Chl-*a*)	µg l^{-1}	156	Other	17	±	42	37	±	79	0.0002	**
Phytoplankton counts	#/ µl	117	Other	26,377	±	63,529	382,552	±	987,599	0.001	*
Chroocales	#/ µl	117	Other	7,650	±	35,107	199,048	±	740,976	0.004	*
Microcystis	#/ µl	117	Other	5,084	±	19,917	118,137	±	617,551	0.449	
Oscillatoriales	#/ µl	117	Other	953	±	2,044	2,363	±	7,462	0.441	
Nostocales	#/ µl	117	Other	8,013	±	42,322	50,807	±	219,176	0.176	
Coelosphaerium	#/ µl	117	Other	398	±	1,415	363	±	1,360	0.856	
Chlorophyta	#/ µl	117	Other	3,695	±	10,785	11,095	±	28,285	0.232	
Euglenophyta	#/ µl	117	Other	148	±	326	326	±	171	0.465	
Chrysophyta	#/ µl	117	Other	82	±	268	58	±	649	0.682	
Diatoms	#/ µl	117	Other	70	±	252	209	±	978	0.545	
Dinophyta	#/ µl	117	Other	16	±	46	63	±	295	0.809	
Cryptophyta	#/ µl	117	Other	254	±	630	78	±	197	0.204	
Unicellular algae < 35 µm	#/ µl	117	Other	5,772	±	34,172	6,184	±	16,201	0.095	
% Cyanobacteria	%	117	Other	68	±	27	77	±	29	0.009	*
Zooplankton											
Total zooplankton (no rotifers)	µg L^{-1}	130	Other	407	±	434	393	±	565	0.267	
Cladocerans	% total	130	Other	64	±	23	50	±	29	0.010	*
Calanoida	% total	130	Other	25	±	10	34	±	13	0.073	~
Cyclopoida	% total	130	Other	11	±	25	11	±	28	0.436	
Large Cladocerans	% clad.	130	Other	59	±	26	69	±	14	0.062	~
Daphnia spp.	% clad.	130	Other	42	±	3	50	±	14	0.110	
Simocephalus	% clad.	130	Other	10	±	31	4	±	28	0.002	**
Diaphanosoma birgei	% clad.	130	Other	7	±	35	15	±	37	0.355	

Chydoridae	% clad.	130	Other	21	±	17	10	±	19	0.003	**
Bosmina	% clad.	130	Other	1	±	15	5	±	26	0.026	*
Ceriodaphnia	% clad.	130	Other	15	±	10	16	±	3	0.914	
Polyphemus pediculus	% clad.	130	Other	4	±	13	1	±	10	0.009	**
Zooplankton richness	#/L	65	Normal	4.7	±	4.3	5.1	±	7.9	0.801	
Macroinvertebrates											
Total macroinvertebrate	µg l^{-1}	63	Log normal	3,730	±	3,519	2,189	±	2,428	0.074	
Predators	µg l^{-1}	63	Log normal	964	±	1,333	409	±	444	0.026	*
Scrapers	µg l^{-1}	63	Other	1,034	±	1,982	352	±	409	0.187	
Gatherer/ collectors	µg l^{-1}	63	Log normal	997	±	1,227	627	±	907	0.094	
Shredders	µg l^{-1}	63	Other	685	±	1,057	772	±	1,667	0.218	
Filterers	µg l^{-1}	63	Other	50	±	132	29	±	112	0.287	
Macroinvertebrate richness	#/ sample	23	Normal	19	±	6	11	±	6	0.029	*
Fish	% presence	156	Other	13	±	0.3	25	±	0	0.087	~
Trophic indices											
Chl-a: TP	ratio	130	Other	0.23	±	0.35	0.35	±	0.58	0.011	*
Cladoceran: Chl-a	ratio	130	Other	53	±	77	26	±	66	0.0002	**

Appendix D. Phytoplankton-rich versus phytoplankton-poor lakes: differences in limnological variables and biological communities.

Mean and standard deviation for physical, chemical and biological variables in phytoplankton-rich and phytoplankton-poor lakes from surveys in August 2001-2007. P-values are from t-tests, Mann-Whitney U tests, or Chi-squared tests as appropriate. * indicates statistical significance at $\alpha = 0.05$, ** indicates statistical significance after a Bonferroni adjustment of $\alpha = 0.05/72 = 0.0007$.

	Units	n	Distribution	Phytoplankton-rich	Phytoplankton-poor	P value	Sign.
Abiotic variables							
Average depth	cm	156	Log normal	79 ± 39	85 ± 33	0.15	
Maximum depth	cm	120	Log normal	112 ± 52	109 ± 46	0.879	
Secchi depth	cm	152	Other	63 ± 35	79 ± 28	0.0006	**
Secchi depth: maximum depth	%	152	Other	76 ± 25	93 ± 14	<0.0001	**
Turbidity	NTU	132	Other	8.2 ± 10.4	3.4 ± 4.1	<0.0001	**
pH	pH units	153	Normal	8.2 ± 1.1	8.3 ± 1.2	0.777	
Electrical conductivity	µS cm^{-1}	153	Other	162.0 ± 82.9	143.1 ± 87.9	0.175	
Dissolved oxygen	mg l^{-1}	126	Other	8.9 ± 3.3	9.1 ± 2.3	0.696	
Total dissolved solids	mg l^{-1}	111	Other	0.11 ± 0.05	0.10 ± 0.04	0.182	
Dissolved organic carbon	mg l^{-1}	130	Other	96.8 ± 132.3	58.2 ± 83.7	0.031	*
Alkalinity	mg l^{-1}	153	Log normal	75.1 ± 38.8	69.3 ± 29.6	0.931	
Bicarbonate	mg l^{-1}	153	Log normal	87.6 ± 47.7	73.5 ± 34.4	0.333	
Total phosphorus	µg l^{-1}	154	Other	162.3 ± 150.4	65.2 ± 60.4	<0.0001	**
Total nitrogen	µg l^{-1}	156	Other	3408 ± 2111	2255 ± 1558	<0.0001	**
TN:TP (mass)	Ratio	154	Other	13.0 ± 8.3	19.0 ± 10.8	<0.0001	**
Total dissolved phosphorus	µg l^{-1}	156	Other	42.6 ± 35.7	36.5 ± 49.4	0.057	~
Soluble reactive phosphorus	µg l^{-1}	130	Other	11.2 ± 15.9	13.2 ± 43.9	0.015	*
Total dissolved nitrogen	µg l^{-1}	130	Other	1853 ± 1202	1677 ± 748	0.826	
Ammonium	µg l^{-1}	156	Other	83 ± 221	110 ± 402	0.314	
Nitrate – Nitrite	µg l^{-1}	153	Other	8.5 ± 11.7	10.2 ± 22.1	0.613	
$(NH_4^+ + NO_3^-)$: SRP	Ratio	133	Other	24.3 ± 91.1	35.5 ± 95.8	0.131	
Chloride	mg l^{-1}	87	Other	2.8 ± 4.7	1.7 ± 3.3	0.152	
Sulphate	mg l^{-1}	86	Other	10.4 ± 9.6	10.0 ± 13.5	0.314	
Sodium	mg l^{-1}	89	Other	3.6 ± 4.1	2.3 ± 1.9	0.038	*
Potassium	mg l^{-1}	89	Log normal	4.4 ± 3.0	3.8 ± 3.5	0.229	
Calcium	mg l^{-1}	89	Normal	25.0 ± 12.1	23.4 ± 11.5	0.549	
Magnesium	mg l^{-1}	89	Other	7.8 ± 4.3	6.9 ± 3.4	0.355	

Iron	mg l^{-1}	75	Other	0.11	±	0.11	0.12	±	0.13	1	
Silica	mg l^{-1}	124	Other	3.3	±	2.8	1.4	±	1.6	0.0002	**
Primary producers											
SAV abundance	Rating	156	Other	2.6	±	1.2	3.4	±	1.0	0.0004	**
SAV abundance	% PVI	18	Normal	28	±	39	47	±	29	0.411	
SAV biomass	g m^{-2}	86	Log normal	48	±	49	52	±	44	0.769	
Periphyton biomass (Chl-a)	µg m^{-2}	23	Log normal	3,161	±	2,609	1,698	±	3,008	0.310	
Periphyton biomass (Fucoxanthin)	µg m^{-3}	23	Other	617	±	1,055	625	±	1,538	0.972	
Periphyton biomass (Lutein)	µg m^{-4}	23	Other	660	±	692	364	±	359	0.857	
Periphyton biomass (Chl-b)	µg m^{-5}	23	Other	377	±	437	268	±	331	0.430	
Periphyton biomass (Violaxanthin)	µg m^{-6}	23	Other	110	±	249	27	±	62	0.649	
Periphyton biomass (total)	µg m^{-7}	23	Log normal	4,924	±	4,342	2,982	±	4,743	0.504	
Phytoplankton biomass (Chl-a)	µg l^{-1}	156	Other	72	±	99	7	±	4	<0.0001	**
Phytoplankton counts	#/ µl	117	Other	484,455	±	1,115,668	32,673	±	95,905	<0.0001	**
Chroocales	#/ µl	117	Other	240,582	±	844,097	17,151	±	84,722	<0.0001	**
Microcystis	#/ µl	117	Other	151,662	±	708,782	6,537	±	31,431	0.955	
Oscillatoriales	#/ µl	117	Other	1,456	±	3,876	1,584	±	5,589	0.465	
Nostocales	#/ µl	117	Other	75,691	±	254,836	2,923	±	8,807	0.035	*
Coelosphaerium	#/ µl	117	Other	400	±	1,438	376	±	1,371	0.577	
Chlorophyta	#/ µl	117	Other	13,777	±	31,920	3,564	±	10,334	0.000	**
Euglenophyta	#/ µl	117	Other	412	±	185	135	±	304	0.333	
Chrysophyta	#/ µl	117	Other	60	±	166	77	±	555	0.734	
Diatoms	#/ µl	117	Other	59	±	1,115	160	±	236	0.075	
Dinophyta	#/ µl	117	Other	43	±	128	33	±	219	0.693	
Cryptophyta	#/ µl	117	Other	304	±	792	123	±	273	0.492	
Unicellular algae < 35 µm	#/ µl	117	Other	8,265	±	18,258	4,871	±	31,533	0.000	**
% Cyanobacteria	%	117	Other	79	±	27	69	±	29	0.006	*
Zooplankton											
Total zooplankton (no rotifers)	µg L^{-1}	130	Other	386	±	367	408	±	539	0.441	
Cladocerans	% total	130	Other	51	±	29	61	±	25	0.068	~
Calanoida	% total	130	Other	33	±	16	28	±	9	0.241	
Cyclopoida	% total	130	Other	14	±	28	9	±	26	0.194	
Large Cladocerans	% clad.	130	Other	74	±	18	58	±	24	0.005	**
Daphnia spp.	% clad.	130	Other	53	±	11	42	±	9	0.134	
Simocephalus	% clad.	130	Other	5	±	25	9	±	31	0.065	~
Diaphanosoma birgei	% clad.	130	Other	16	±	38	8	±	35	0.306	
Chydoridae	% clad.	130	Other	11	±	16	19	±	18	0.015	*
Bosmina	% clad.	130	Other	3	±	29	2	±	15	0.630	

Ceriodaphnia	% clad.	130	Other	12	±	5	17	±	8	0.2	
Polyphemus pediculus	% clad.	130	Other	1	±	10	3	±	13	0.038	*
Zooplankton richness	#/L	65	Normal	4.6	±	4.3	4.9	±	6.6	0.838	
Macroinvertebrates											
Total macroinvertebrate	μg l^{-1}	63	Log normal	3,240	±	3,391	3,169	±	3,217	0.968	
Predators	μg l^{-1}	63	Log normal	768	±	1,149	771	±	1,139	0.692	
Scrapers	μg l^{-1}	63	Other	789	±	1,791	799	±	1,592	0.658	
Gatherer/ collectors	μg l^{-1}	63	Log normal	841	±	1,208	880	±	1,109	0.843	
Shredders	μg l^{-1}	63	Other	794	±	1,615	679	±	1,127	0.506	
Filterers	μg l^{-1}	63	Other	49	±	124	40	±	126	0.884	
Macroinvertebrate richness	#/ sample	23	Normal	18	±	7	17	±	7	0.915	
Fish	% presence	156	Other	14	±	0.3	19	±	0	0.600	
Trophic indices											
Chl-a: TP	ratio	130	Other	0.63	±	0.75	0.14	±	0.10	< 0.0001	**
Cladoceran: Chl-a	ratio	130	Other	5	±	9	56	±	82	< 0.0001	**

Appendix E. Surficial geology types: key differences in lake and landscape variables.

Differences in surficial geology types for landscape and lake variables determined by Kruskal Wallis tests. Average and standard deviation values are presented.

	Units	Glaciofluvial	Morainal	Organic	*P*-value	Sign.
Area	ha	17 ± 18.4	4.5 ± 3.1	13.5 ± 8.3	0.035	*
Shoreline/ volume	ratio	0.022 ± 0.017	0.028 ± 0.014	0.013 ± 0.004	0.022	*
Dynamic ratio	ratio	443.4 ± 264	288.6 ± 149.2	462.9 ± 200.2	0.211	
Elevation	m	665.4 ± 5.4	667.1 ± 5.3	649.6 ± 5.6	0.0006	**
Wetland in 300m buffer	%	34.7 ± 20.9	38.9 ± 15	62.8 ± 8.3	0.005	*
Average depth	cm	88.2 ± 37.4	74 ± 23.7	84.2 ± 26.6	0.657	
Max. depth	cm	120.5 ± 49.5	101.9 ± 52.1	97.2 ± 20.3	0.344	
Light penetration	%	87 ± 4	92 ± 12	85 ± 8	0.235	
Turbidity	NTU	5 ± 4.1	4.4 ± 2.3	4.3 ± 2.5	0.920	
DOC	mg L^{-1}	50.3 ± 32.9	69.8 ± 35.1	78.9 ± 37.2	0.265	
EC	µS cm^{-1}	111.2 ± 40.1	136.4 ± 50.3	186.9 ± 53.1	0.034	*
Alkalinity	mg L^{-1}	65.6 ± 28.0	62.6 ± 23.6	80.3 ± 25.1	0.314	
TP	µg L^{-1}	85.7 ± 104.0	78.0 ± 111.6	113.5 ± 97	0.230	
TN	mg L^{-1}	1921.0 ± 1953.1	2624.2 ± 1319.4	3061.9 ± 1845	0.014	*
N:P (mass)	Ratio	16 ± 5	21 ± 8	15 ± 2	0.255	
Chloride	mg L^{-1}	0.4 ± 0.3	1.4 ± 2.1	3.9 ± 4.2	0.018	*
Sulphate	mg L^{-1}	1.6 ± 14.0	11.5 ± 3.7	15.6 ± 11.9	0.005	**
Sodium	mg L^{-1}	2.3 ± 1.0	1.9 ± 0.9	3.8 ± 2.4	0.186	
Potassium	mg L^{-1}	3.0 ± 3.4	4.3 ± 2.0	4.3 ± 2.5	0.322	
Calcium	mg L^{-1}	19.1 ± 8.1	22.9 ± 11.0	29.3 ± 8.4	0.085	
Magnesium	mg L^{-1}	5.4 ± 3.1	7.0 ± 3.2	8.8 ± 3.5	0.180	
Calcium + Magnesium	mg L^{-1}	24.5 ± 10.5	29.9 ± 13.7	38.2 ± 11.6	0.155	
Iron	mg L^{-1}	0.13 ± 0.1	0.08 ± 0.1	0.14 ± 0.2	0.722	
Silica	mg L^{-1}	2.1 ± 1.4	1.3 ± 1.2	2.3 ± 1.8	0.269	
SAV rating	rating (/5)	3.1 ± 0.8	3.2 ± 0.5	3.1 ± 0.7	0.915	
Chl-a	µg L^{-1}	34.9 ± 41.2	18.1 ± 20	28.3 ± 26.7	0.207	
Fish	sum of years	55 ± 48	0 ± 0	0 ± 0	0.001	**
Phyto. rich regime persistence	% of years	35 ± 34	25 ± 16	30 ± 22	0.910	
SAV rich regime persistence	% of years	51 ± 22	64 ± 25	56 ± 24	0.559	

Appendix F. Study lakes: key landscape variables (mean ± standard deviation).

Lake id	Surficial geology class	Surface water connectivity	% Wetland in 100m buffer	Area (ha)	Perimeter (m)	Perimeter: area ratio	Average depth (cm)			Maximum depth (cm)			Volume (m3)	Perimeter : volume ratio	Shoreline : volume ratio	Dynamic ratio (sqrt area/ av. depth)	Elevation (m)
1	Glaciofluvial	Flowthrough	66.3	9.5	2315.7	0.024	55	±	40	138	±	43	51902	0.024	0.024	560	669
7	Moraine	Isolated	11.8	5.4	939.4	0.017	118	±	21	93	±	19	63554	0.017	0.017	197	670
11	Moraine	Isolated	62.6	0.9	342.2	0.039	92	±	16	67	±	16	8174	0.039	0.039	102	670
15	Glaciofluvial	Isolated	14.4	1.5	839.1	0.056	34	±	9	38	±	1	5156	0.056	0.056	358	671
16	Glaciofluvial	Flowthrough	25.5	44.5	2984.9	0.007	87	±	18	111	±	11	386830	0.007	0.007	766	666
19	Glaciofluvial	Isolated	7.5	2.2	609.9	0.028	132	±	24	103	±	23	28396	0.028	0.028	112	672
27	Moraine	Isolated	35.5	8.7	1328.1	0.015	49	±	21	71	±	18	42893	0.015	0.015	596	664
39	Moraine	Isolated	46.7	7.9	1506.0	0.019	90	±	15	172	±	17	71101	0.019	0.019	313	663
42	Moraine	Isolated	38.7	2.3	572.8	0.025	58	±	28	196	±	27	13078	0.025	0.025	259	666
43	Moraine	Isolated	26.9	1.0	560.8	0.056	55	±	19	61	±	22	5492	0.056	0.056	183	673
48	Moraine	Isolated	43.2	3.2	1166.6	0.036	60	±	19	84	±	20	19460	0.036	0.036	298	673
59	Organic	Isolated	45.6	28.9	2432.4	0.008	72	±	24	67	±	21	209061	0.008	0.008	745	649
111	Moraine	Isolated	46.0	6.3	1254.9	0.020	70	±	12	72	±	20	43798	0.020	0.020	360	658
112	Organic	Outflow	70.3	4.9	1046.5	0.022	113	±	15	112	±	40	54825	0.022	0.022	195	647
118	Organic	Isolated	69.2	9.2	1272.3	0.014	56	±	22	132	±	19	52214	0.014	0.014	538	646
121	Organic	Isolated	58.5	8.1	1029.6	0.013	71	±	19	105	±	24	57538	0.013	0.013	402	643
122	Organic	Isolated	69.0	9.0	1207.0	0.013	135	±	24	93	±	27	121774	0.013	0.013	222	644
168	Organic	Flowthrough	59.3	13.8	1533.2	0.011	87	±	16	105	±	23	119754	0.011	0.011	426	655
171	Organic	Isolated	63.9	10.8	1254.2	0.012	71	±	21	80	±	25	76632	0.012	0.012	466	655
201	Glaciofluvial	Flowthrough	33.7	41.3	2657.9	0.006	82	±	23	175	±	42	339093	0.006	0.006	784	660
205	Organic	Isolated	67.0	23.4	1734.5	0.007	68	±	38	85	±	46	146826	0.014	0.014	709	658
206	Glaciofluvial	Flowthrough	43.9	15.5	2155.9	0.014	137	±	41	181	±	45	213411	0.014	0.014	287	660
208	Glaciofluvial	Outflow	52.0	4.5	790.7	0.017	90	±	15	98	±	13	40766	0.017	0.017	237	660

Appendix G. Study lakes: key limnological variables (mean ± standard deviation).

Lake id	SAV rating (/5)			Chl-a (µg L-1)			SAV biomass (g m-2)			Secchi depth (cm)			Secchi/ Max. depth (%)			Electric conductivity (µS cm-1)			pH		
1	2.4	±	1.1	30.5	±	58.7	23.2	±	15.1	104	±	50	87	±	14	110.1	±	110.1	8.5	±	1.0
7	3.9	±	0.8	5	±	6.3	47.7	±	36.7	74	±	21	100	±	0	93.4	±	93.4	8.3	±	0.7
11	3.4	±	0.7	7.6	±	6.2	47.3	±	25.5	56	±	18	100	±	10	113.6	±	113.6	8.4	±	1.1
15	2.4	±	1.8	123.9	±	158.1		±		32	±	4	87	±	24	38.1	±	38.1	6.7	±	1.7
16	3.4	±	1.3	10.1	±	8.2	78.0	±	50.0	83	±	17	91	±	22	150.9	±	150.9	9	±	1.3
19	4.1	±	0.9	7.8	±	5.5	58.0	±	43.8	68	±	9	94	±	17	92.7	±	92.7	7.6	±	1.1
27	3	±	0.9	5.9	±	6.1	12.6	±	6.1	60	±	23	100	±	21	105.7	±	105.7	8.1	±	1.0
39	2.5	±	1.2	39.1	±	38.3	40.3	±	38.3	100	±	40	70	±	31	213.2	±	213.2	8.2	±	0.8
42	2.7	±	0.9	11	±	9.5	29.8	±	21.7	112	±	23	83	±	0	70	±	70.0	7.2	±	1.1
43	3.1	±	0.8	7.9	±	11.0	26.1	±	18.2	55	±	19	100	±	0	175.7	±	175.7	8.7	±	1.9
48	3.1	±	1.2	59.2	±	86.2	25.1	±	15.7	49	±	20	84	±	30	132.2	±	132.2	7.6	±	1.3
59	3.5	±	1.2	14.8	±	11.2	53.8	±	33.4	56	±	24	99	±	0	109.5	±	109.5	8.2	±	1.0
111	3.8	±	0.7	9.4	±	13.0	34.3	±	9.2	61	±	13	100	±	12	187	±	187.0	8.7	±	0.7
112	2.1	±	1.1	39.1	±	51.2	26.7	±	11.1	66	±	35	73	±	18	257.2	±	257.2	8.5	±	1.1
118	3	±	0.7	9.9	±	4.2	33.2	±	30.2	78	±	8	83	±	19	125.3	±	125.3	7.3	±	0.4
121	3.3	±	1.3	13.9	±	20.0	87.9	±	66.9	80	±	17	90	±	26	158.9	±	158.9	8.3	±	1.3
122	2.9	±	0.8	33.8	±	15.5	46.4	±	20.3	61	±	20	79	±	25	240.3	±	240.3	8.6	±	1.2
168	3.6	±	0.7	17.3	±	23.1	108.5	±	85.2	84	±	28	88	±	0	220.8	±	220.8	8.9	±	0.8
171	4	±	0.4	9	±	10.8	98.1	±	98.3	64	±	25	89	±	23	200.7	±	200.7	8.5	±	1.3
201	2.5	±	1.4	19.2	±	19.4	60.1	±	39.0	92	±	22	80	±	23	103.7	±	103.7	9	±	0.5
205	2.4	±	1.1	88.6	±	210.9	41.0	±	39.8	57	±	19	81	±	18	182.3	±	182.3	8.1	±	0.8
206	2.9	±	1.2	10.9	±	4.6	27.0	±	16.4	115	±	42	89	±	18	157.2	±	157.2	7.7	±	0.7
208	4.4	±	0.9	42.3	±	42.7	102.2	±	16.4	75	±	16	85	±	2	125.6	±	125.6	9.1	±	1.0

Lake id	Dissolved oxygen (mg L-1)			TDS (mg L-1)			Turbidity (NTU)			TP (µg L-1)			TDP (µg L-1)			SRP (µg L-1)			TN (µg L-1)		
1	9.3	±	2.3	0.1	±	0.0	1.8	±	20.0	119.8	±	139.4	14.4	±	7.4	5.1	±	3.0	1995	±	1995
7	8.9	±	2.4	0.09	±	0.0	7	±	1.8	49	±	26.1	23.6	±	9.5	3.7	±	4.0	2105	±	2105
11	10	±	3.4	0.09	±	0.0	2.5	±	2.0	45	±	8.7	23.2	±	10.5	2.9	±	1.5	2074	±	2074
15	6.2	±	3.3	0.01	±	0.0	12.3	±	7.8	239.3	±	305.8	29.1	±	17.9	6.1	±	5.3	2256	±	2256
16	10.3	±	2.4	0.1	±	0.0	1.8	±	4.1	48.8	±	18.8	14.8	±	4.5	4.3	±	1.8	1729	±	1729
19	8.3	±	2.6	0.09	±	0.0	5.8	±	5.3	86.3	±	34.1	41.6	±	21.8	11.5	±	7.0	2031	±	2032
27	8.9	±	3.8	0.09	±	0.0	2.8	±	0.7	38.2	±	17.9	15.6	±	5.2	2.6	±	1.8	3058	±	3058
39	9.3	±	3.4	0.12	±	0.0	7.6	±	9.7	112.3	±	38.4	43.1	±	17.4	16.3	±	6.4	2563	±	2563
42	8.8	±	2.1	0.02	±	0.0	1.9	±	2.1	47.4	±	10.0	30.4	±	17.1	5.7	±	5.5	1206	±	1206
43	8.3	±	1.7	0.13	±	0.1	6.6	±	1.8	144.5	±	235.3	36.5	±	26.4	2.8	±	2.3	3857	±	3857
48	5.9	±	2.3	0.08	±	0.0	4.2	±	2.7	125.6	±	146.8	50.2	±	43.7	6.5	±	7.8	3323	±	3323
59	10	±	2.3	0.09	±	0.0	7.2	±	1.6	85.2	±	81.8	28	±	13.7	2.6	±	1.8	2691	±	2691
111	8.8	±	2.5	0.12	±	0.0	2.8	±	3.0	53	±	34.3	27.7	±	14.9	4.3	±	3.0	2527	±	2527
112	8.8	±	3.8	0.17	±	0.0	6.1	±	3.4	145.2	±	131.8	31.9	±	6.9	8.4	±	3.9	3730	±	3730
118	9.1	±	1.8	0.08	±	0.0	3.8	±	2.8	58.9	±	11.7	30.4	±	11.4	7.8	±	6.8	1975	±	1975
121	9.4	±	2.9	0.09	±	0.0	7.8	±	7.9	62	±	26.1	31.4	±	11.3	5.7	±	3.7	2028	±	2028
122	10.7	±	3.7	0.14	±	0.0	2	±	3.3	94.6	±	31.4	32.5	±	7.4	7	±	2.2	3305	±	3305
168	10.4	±	1.8	0.17	±	0.0	1.4	±	8.8	138.9	±	87.8	78.8	±	28.1	33.7	±	27.2	3685	±	3685
171	8.6	±	1.8	0.11	±	0.0	4	±	1.4	86.1	±	41.6	62.9	±	30.8	12.5	±	7.5	2850	±	2850
201	10.8	±	1.7	0.09	±	0.0	2	±	6.6	55.7	±	17.8	14.3	±	2.4	2.4	±	1.7	1879	±	1879
205	7.3	±	2.3	0.09	±	0.0	2.2	±	3.1	234.4	±	147.6	193.4	±	128.9	147.5	±	147.5	4264	±	4264
206	8.6	±	0.6	0.1	±	0.0	8.6	±	2.9	39.1	±	17.6	13.1	±	4.4	2	±	2.0	1712	±	1712
208	9.2	±	3.3	0.08	±	0.0	2.6	±	4.3	71.4	±	28.8	22.4	±	8.1	4.7	±	4.2	1966	±	1966

Lake id	TDN (μg L-1)			NO3 (μg L-1)			NH4 (μg L-1)			TN:TP			Avail N:P			DOC (mg L-1)			ALK (μeq L-1)		
1	750	±	750.0	6.8	±	8.8	11	±	6.6	15	±	19.2	6	±	6.1	16.2	±	9.6	69.1	±	16.2
7	2084	±	2084.4	8.3	±	8.2	529	±	1339.0	20	±	7.7	151	±	282.3	25.5	±	2.9	46.3	±	10.8
11	1857	±	1856.8	20.9	±	39.6	89.5	±	122.2	21	±	4.3	74	±	107.5	131.9	±	197.9	53.2	±	10.2
15	942	±	942.4	3.8	±	2.4	2	±	1.0	9	±	6.4	4	±	4.7	19.8	±	2.0	16.1	±	3.6
16	1370	±	1370.3	5.2	±	6.0	175.3	±	322.3	18	±	7.6	62	±	109.2	36.9	±	37.0	97.4	±	44.9
19	1416	±	1415.7	18.8	±	38.4	37.7	±	45.8	11	±	3.0	4	±	4.4	78.5	±	140.8	47.1	±	17.3
27	2283	±	2282.8	4.9	±	6.9	172.9	±	423.6	37	±	13.9	98	±	218.2	32.8	±	9.5	56.7	±	16.2
39	1073	±	1072.7	4.5	±	5.5	27.1	±	20.4	10	±	6.0	2	±	1.6	100.8	±	165.9	104.5	±	39.7
42	1048	±	1048.0	4.6	±	4.2	44.6	±	89.8	12	±	4.0	8	±	7.5	84.8	±	149.9	30.8	±	17.5
43	2220	±	2219.6	5.6	±	11.6	16.2	±	11.0	24	±	10.7	16	±	18.9	61.8	±	9.9	73.4	±	38.8
48	2325	±	2324.7	9.2	±	13.4	141	±	324.2	17	±	6.9	14	±	15.5	56.4	±	39.6	51.3	±	25.9
59	2103	±	2102.5	6.8	±	10.2	26	±	33.3	19	±	7.3	31	±	46.9	45	±	9.2	53.4	±	13.4
111	2159	±	2159.0	5.5	±	6.7	71.1	±	117.7	24	±	5.2	23	±	26.0	64.5	±	61.2	84.7	±	17.1
112	1678	±	1678.2	11.4	±	11.6	32.4	±	26.4	13	±	2.4	8	±	9.6	151.5	±	159.6	108.1	±	18.0
118	1607	±	1607.3	13.9	±	20.5	69.6	±	77.2	16	±	5.7	22	±	25.8	102.7	±	148.0	55.4	±	27.0
121	1424	±	1424.5	17.2	±	22.3	139.6	±	325.1	16	±	4.7	21	±	32.0	97.3	±	127.6	69.1	±	22.5
122	2581	±	2581.1	10.2	±	8.7	21.7	±	16.8	17	±	3.0	5	±	2.5	51	±	10.9	117.5	±	28.3
168	2396	±	2396.4	3.9	±	3.9	28.5	±	33.0	15	±	10.5	2	±	2.0	54	±	12.0	98.3	±	22.2
171	2016	±	2016.5	5.3	±	4.6	23.2	±	21.6	15	±	4.4	3	±	3.0	82	±	67.1	82	±	11.6
201	1191	±	1190.8	7.5	±	10.5	35.1	±	45.2	17	±	11.6	52	±	81.6	82.9	±	146.9	72.5	±	19.1
205	2327	±	2327.5	42.6	±	63.3	534.6	±	738.1	12	±	8.9	7	±	8.4	47.7	±	4.8	58.6	±	8.4
206	1310	±	1310.5	4.4	±	1.7	86	±	74.4	25	±	20.1	114	±	176.7	25.4	±	3.5	94.5	±	23.9
208	1261	±	1261.1	5.3	±	6.8	29.6	±	29.7	15	±	7.6	10	±	4.6	92.2	±	164.0	62.2	±	30.0

Lake id	Bicarb (mg L-1)			Carb (mg L-1)			Cl (mg L-1)			SO4 (mg L-1)			Na (mg L-1)			K (mg L-1)			Ca (mg L-1)		
1	80.6	±	23.4	1.8	±	2.2	0.3	±	0.3	2.3	±	3.8	4.1	±	6.2	0.3	±	0.3	24	±	7.1
7	53.4	±	15.6	1.5	±	2.7	0.2	±	0.2	5.9	±	2.1	1.6	±	0.7	4	±	1.9	13.8	±	2.6
11	56.3	±	12.5	4.2	±	6.6	0.1	±	0.1	20.5	±	6.5	1.1	±	0.4	0.5	±	0.4	25	±	6.0
15	19.6	±	4.4	0	±	0.0	0.1	±	0.1	0.2	±	0.0	1	±	0.9	3.9	±	2.1	4.3	±	0.9
16	97.9	±	68.5	10.3	±	10.0	0.2	±	0.2	0.7	±	0.4	2.6	±	1.7	1.7	±	0.7	26.7	±	21.4
19	60.4	±	16.6	0.8	±	1.3	1.1	±	1.1	6.6	±	7.5	1.4	±	0.7	10.2	±	5.8	13.2	±	4.3
27	65.4	±	15.8	0	±	0.0	0.4	±	0.4	7.2	±	10.2	1.7	±	0.8	5.5	±	3.5	17.5	±	5.1
39	142.2	±	33.4	1.1	±	2.6	0.3	±	0.3	6.1	±	1.7	2.9	±	1.2	3.8	±	1.1	36.7	±	4.5
42	29.7	±	3.7	0	±	0.0	0.4	±	0.4	0.5	±	0.3	0.9	±	0.6	6.6	±	2.0	5.5	±	0.6
43	74.9	±	32.5	1.9	±	3.0	0.4	±	0.4	25.5	±	19.9	1.4	±	1.0	2.8	±	2.2	37.2	±	16.8
48	49.5	±	11.6	0	±	0.0	4.5	±	4.5	26.2	±	24.6	2.5	±	2.9	4.9	±	3.7	20.1	±	11.3
59	66.5	±	17.0	1.3	±	1.9	2.6	±	2.6	4	±	1.3	2.4	±	1.5	5	±	3.1	19.8	±	5.2
111	102.3	±	41.9	5.4	±	8.2	5.2	±	5.2	6.1	±	2.1	3.3	±	0.9	6.6	±	2.4	27.4	±	7.4
112	123.1	±	24.4	4.5	±	5.7	5.3	±	5.3	28.5	±	4.3	7.7	±	9.0	4.9	±	1.8	39.5	±	6.7
118	54.3	±	9.4	0.7	±	1.7	0.4	±	0.4	3.7	±	1.8	1.4	±	0.6	5	±	1.1	14.8	±	0.5
121	69.6	±	26.9	6	±	10.6	0.5	±	0.5	12.9	±	4.7	1.8	±	1.3	0.9	±	0.6	27.6	±	3.9
122	114.9	±	62.4	14.8	±	18.3	0.4	±	0.4	14	±	7.9	3.8	±	1.6	7.5	±	1.9	31.8	±	10.2
168	94.4	±	32.5	17.9	±	20.0	11.8	±	11.8	20	±	4.1	6.9	±	2.2	7.4	±	4.5	36.8	±	1.8
171	77.7	±	21.6	10.5	±	13.8	8.1	±	8.1	16.2	±	5.4	4.8	±	2.6	2	±	1.9	33.9	±	3.5
201	87.5	±	35.6	4.1	±	6.1	0.5	±	0.5	0.2	±	0.3	2.9	±	0.9	2.5	±	1.0	23.6	±	6.8
205	63.1	±	17.3	5.3	±	8.8	2	±	2.0	29	±	26.4	1.9	±	0.4	1.7	±	1.6	30.4	±	8.5
206	106.8	±	16.6	0.3	±	0.7	0.3	±	0.3	0.3	±	0.4	2.1	±	1.0	2.1	±	0.8	24.7	±	6.6
208	56.2	±	11.8	2.9	±	4.1	0.1	±	0.1	0.2	±	0.3	2.1	±	0.7	0.8	±	0.3	17	±	1.6

Lake id	Mg (mg L-1)			Fe (mg L-1)			Si (mg L-1)		
1	3.4	±	0.6	0.1	±	0.1	4.1	±	1.5
7	6.2	±	3.6	0.2	±	0.1	0.4	±	0.5
11	5	±	0.8	0.1	±	0.0	1.4	±	1.1
15	1.8	±	0.8	0.3	±	0.1	0.2	±	0.1
16	10.7	±	1.4	0.1	±	0.1	3.1	±	1.8
19	4.7	±	2.2	0.1	±	0.1	0.4	±	0.4
27	5.1	±	1.2	0.1	±	0.0	0.4	±	0.1
39	11.8	±	1.0	0.1	±	0.0	3.6	±	3.0
42	2.3	±	0.4	0.1	±	0.0	0.1	±	0.1
43	8.6	±	3.2	0	±	0.0	2.1	±	1.5
48	6.1	±	2.3	0.1	±	0.1	0.6	±	0.4
59	5	±	1.1	0.1	±	0.1	0.8	±	0.6
111	10.6	±	2.3	0	±	0.0	1.6	±	2.5
112	11.9	±	1.8	0	±	0.0	6.1	±	2.1
118	4.4	±	0.7	0.2	±	0.2	0.7	±	0.5
121	7.1	±	1.5	0.1	±	0.1	1.7	±	1.4
122	12.9	±	1.1	0.1	±	0.0	3.5	±	2.2
168	13.1	±	3.2	0	±	0.0	2.4	±	4.2
171	9.8	±	2.1	0.1	±	0.1	0.7	±	0.9
201	7.3	±	0.7	0.1	±	0.1	2.8	±	1.3
205	6.5	±	2.0	0.5	±	0.3	2.2	±	2.0
206	6.8	±	1.0	0	±	0.0	1.9	±	0.5
208	3	±	0.3	0.2	±	0.1	2.3	±	2.1