

Frequent regime shifts in trophic states in shallow lakes on the Boreal Plain: Alternative “unstable” states?

S. E. Bayley

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

I. F. Creed

Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada

Department of Geography, University of Western Ontario, London, Ontario N6A 5C2, Canada

G. Z. Sass

Department of Geography, University of Western Ontario, London, Ontario N6A 5C2, Canada

A. S. Wong

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Abstract

Shallow lakes are known to exhibit alternative states in their biotic structure. Lakes dominated by submersed aquatic vegetation (SAV) are “clear,” while lakes dominated by algae (high concentrations of chlorophyll *a* [Chl *a*]) are “turbid.” The roles of total phosphorus (TP) and SAV in defining these alternative states were examined for up to 6 yr in 24 naturally eutrophic shallow lakes (12.4–670.4 $\mu\text{g TP L}^{-1}$) with variable SAV cover (0–100%) on the western Boreal Plain in Alberta, Canada. Clear lakes had $<18 \mu\text{g Chl } a \text{ L}^{-1}$. Sixty-seven percent of lakes were clear in any given year, but individual lakes did not remain clear over consecutive years. While 29% did not switch, 71% of lakes were unstable, with 57% switching states once and 14% switching more than once. To increase the temporal and spatial scale of analysis, we used Landsat Thematic Mapper satellite imagery (1984–2003) to classify clarity for up to 20 yr in 82 naturally eutrophic shallow lakes. Approximately 80% of lakes were unstable, with 7% switching once and more than 73% switching 2–9 times. Only 20% of lakes were stable and clear. Switches in lake clarity were related to TP but were also dependent on the abundance of SAV. For lakes with high SAV, the TP threshold for the transition from clear to turbid was $275 \mu\text{g TP L}^{-1}$, while for lakes with low SAV, the TP threshold was $50 \mu\text{g TP L}^{-1}$. Given the harsh winter conditions, including lakes with ice depths of up to 0.7 m and anoxia leading to winterkill of aquatic communities, these systems are strongly abiotically regulated and lack mechanisms that maintain a lake in a stable state.

Alternative stable states theory postulates that ecosystems can manifest two different stable states under similar conditions (Scheffer et al. 2001). In shallow-lake ecosystems, alternative stable states theory may be expressed as the dominance of either turbid, algal-dominated lakes or clear, submersed aquatic vegetation (SAV) dominated lakes (Scheffer et al. 1993). These alternate states offer substantially different physical, chemical, and biological conditions for the biota living in these aquatic systems and are thus key to our understanding of the trophic dynamics of these systems (Beisner et al. 2003). This paper combines ground- and satellite-based analyses to examine

the relevance of this theoretical perspective in both spatial and temporal aspects in shallow lakes on the western Boreal Plain.

Alternative stable states have been described in many shallow-lake studies over the past 20 yr (Scheffer and Jeppesen 1998; Carpenter et al. 1999). The mechanisms associated with the maintenance of alternative stable states have been described extensively for some lakes (Blindow et al. 1993; Hargeby et al. 1994). In algal-dominated lakes, the lack of SAV promotes resuspension of bottom sediments, remobilization of nutrients from bottom sediments, enhanced nutrients available for algal growth, and the lack of a refuge for algal-grazing zooplankton (Scheffer 1998). Algal-dominated lakes exhibit rapid uptake and re-release of phosphorus by algae leading to the formation of dense algal blooms that create turbid conditions that shade out SAV growth (Carpenter and Lodge 1986; Scheffer et al. 1993; Moss et al. 1994). In contrast, in SAV-dominated lakes, SAV reduces resuspension of bottom sediments and provides a refuge for algal-grazing zooplankton (Scheffer 1998).

Previous studies have shown that alternative stable states are relatively stable over time, with lakes remaining in

Acknowledgments

We thank members of the Hydrology, Ecology And Disturbance (HEAD) research group (specifically A. L. Foote and K. J. Devito), Ducks Unlimited Canada (specifically E. Butterworth), our industrial partners (Weyerhaeuser Company, Alberta Pacific Forest Industries, Syncrude Canada), and a Collaborative Research and Development-Natural Sciences and Engineering Research Council (CRD-NSERC) grant to the HEAD research group. T. Hebben and A. Asselin provided field and technical assistance, and J. I. Norlin provided discussion and comments on the manuscript.

either a clear, SAV-dominated state, or a turbid, algal-dominated state for several years to decades (Giles 1987; Blindow et al. 1993; Scheffer et al. 1993). It has been suggested that only strong perturbations are sufficient to cause the alternative stable states to switch to another state (Blindow 1992; Scheffer 1998; Takamura et al. 2003). These studies were largely conducted in lakes located in managed landscapes in temperate climates (Scheffer 1998), although there are some studies of more tropical (Bachmann et al. 2002) or boreal (Jeppesen et al. 2003) climates. Scheffer (1998) postulated that prior to human development most shallow lakes remained in a clear state and only with the advent of human disturbance did large numbers of lakes become turbid with cultural eutrophication being a major influence affecting alternative stable states (Scheffer 1998). Noges et al. (2003) studied 86 lakes across a broad latitudinal gradient and found that the single most important determinant for shallow-lake water chemistry (including total phosphorus [TP], total nitrogen [TN], and chlorophyll *a* [Chl *a*]) was cultural eutrophication.

More recent analyses have noted that ecological systems are by nature dynamic and many systems have frequent regime shifts, only some of which can be designated as “text-book” examples of alternative stable states (e.g., Scheffer et al. 2001; Scheffer and Carpenter 2003; Schröder et al. 2005). Shifts between different ecological regimes can be rapid or possess a long period of transition making it difficult to demonstrate the existence of alternative stable states. Scheffer and Carpenter (2003) suggest three approaches that can be used to indicate alternative stable states in field data. These include a jump in a time series (e.g., abrupt change in Chl *a* concentration over time), multimodality of frequency distribution of states, and a dual relationship to control factors. However, none of these approaches is truly conclusive in that ecosystems can be affected by some environmental factor or event that is unrelated to the shifts in state or regime (Scheffer and Carpenter 2003).

In this study, we focus on lakes that are naturally high in nutrients and have minimal human disturbance. Shallow lakes in the central portion of the Boreal Plain of western Canada provide habitat for millions of water birds and represent one of the most important breeding habitats for water birds in North America (Ducks Unlimited Canada unpubl. data). Because of the vital role alternate states play in the productivity of lakes, we need a greater understanding of what the dominant states are, what the processes are that control their formation, and how stable they are once they are formed in lakes. A recent study by Bayley and Prather (2003) provided evidence for the existence of alternative states based on a synoptic survey of lakes on the Boreal Plain of western Canada; however, the stability of these alternative states was not examined. Since long-term data on lakes are scarce in this remote landscape, newer techniques to examine large spatial scales and long temporal scales are needed to further the investigation of the occurrence and stability of alternative states.

In this paper, we investigate the spatial and temporal distribution of Chl *a* (as a proxy for algal biomass) and SAV in the naturally nutrient-rich shallow lakes of the region, and look for evidence of alternative stable states.

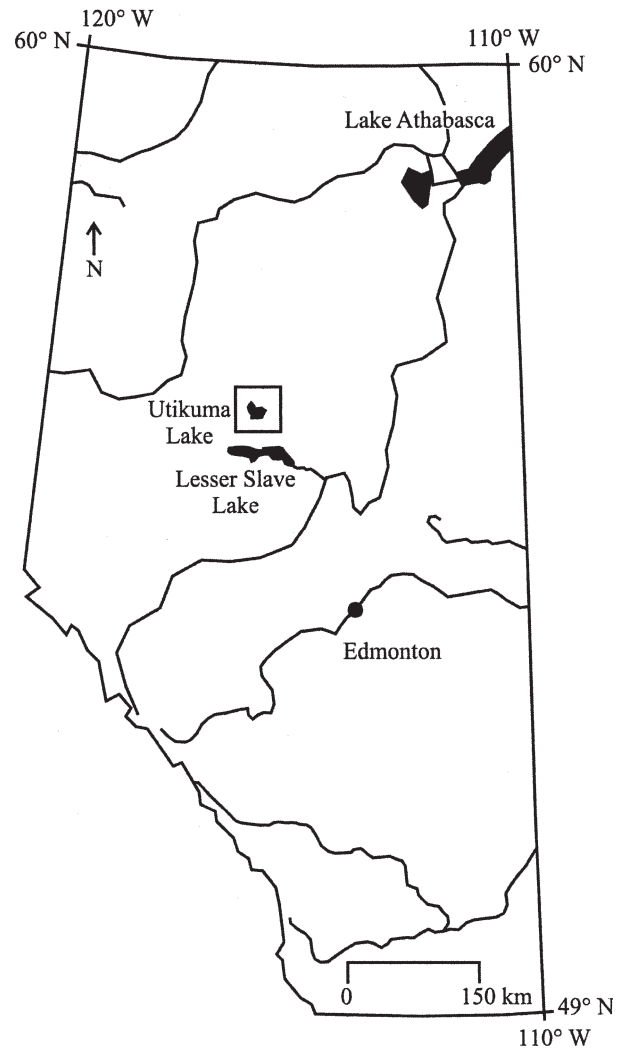


Fig. 1. Map of study area located in central Alberta, Canada ($56^{\circ}00'N$, $115^{\circ}30'W$). The Utikuma study area is shown by a square.

We use ground-based surveys of concentration of Chl *a* to convert red band reflectance of Landsat Thematic Mapper satellite imagery to Chl *a* and then examine the proportion and stability of clear and turbid lakes in 82 lakes over a 20-yr period. We explore whether these lakes have alternative stable states using the three approaches described above. Finally, we examine the relationships of abiotic factors with alternative states to identify possible controls on clear versus turbid lakes in this landscape.

Methods

Study area—The study area is situated in north central Alberta ($56^{\circ}00'N$, $115^{\circ}30'W$) surrounding Utikuma Lake, Alberta (Fig. 1). The area is located in the central mixed-wood subregion of the boreal forest and is composed of peat-forming bogs and fens as well as swamps and marshes. Our study area covers ~ 600 km² and is composed of three major glacial landforms: outwash plain (undulating areas with sand), moraine (hummocky areas with silt and clay),

and lacustrine plain (undulating areas with clay and extensive peatlands). See Bayley and Prather (2003) for a more detailed description of the study area.

Shallow lakes in this region experience harsh climatic conditions. The region is characterized by long cold winters and short warm summers with a mean annual temperature of 1.7°C. The shallow lakes freeze in October–November, reaching a maximum ice depth of 0.50–0.70 m by late winter. The lakes generally thaw in April, although the marsh and fen wetland fringe around the open water often does not thaw until late May or June. Since lake depths are typically ~1 m, the water beneath the ice is anoxic for much of the winter leading to winterkill and mostly fishless lakes (Zimmer et al. 2001; Conlon 2002; Tonn et al. 2004).

In these shallow lakes, algae start to grow quickly in May of each year (after ice-out), while SAV growth is typically slower. SAV rarely persists in sediment over winter, and the rooted vegetative growth is resupplied from floating fragments that start to grow in late May or June. Thus, these lakes are “reset” each year in terms of their vegetative state and contain very little rooted submersed vegetation that persists from year to year. In addition to lack of persistence in SAV, free-swimming zooplankton (*Daphnia* sp.) are known to be reduced by the anoxic conditions over winter, which affects the grazing pressure on algae in spring (Isermann et al. 2004). The fragments of plants and eggs and larval forms of zooplankton and macroinvertebrates can provide the potential to repopulate the system as the weather warms. Thus, not only is the vegetation reset, but the grazers can be “reset” as well. With the advancing growing season and warmer temperatures, the lakes become either clear or turbid by summer (i.e., late July or August).

Lake characteristics based on in situ measurements—Two sampling strategies were employed to establish lake characteristics: spatially extensive and temporally intensive. A synoptic survey of 97 lakes was conducted in 2001 primarily by helicopter. An intensive survey of 24 lakes (17 of which were part of the synoptic survey) was conducted as part of a multiyear monitoring program from 2000–2005; two of these lakes dried up periodically and were therefore not sampled during those years. All lakes were sampled to capture the summer algal biomass in August.

In the ground-based surveys (consisting of the 2001 synoptic- and 2000–2005 intensive-lake surveys), lakes were surveyed for physical, chemical, and biological factors by helicopter and/or boat (at their center, which was assumed to be the deepest part of the lake). Physical factors, specifically, depth at the center of the lake, Secchi disk depth, and turbidity, were measured. The chemical factors measured included the concentration of phosphorus (total phosphorus [TP], total dissolved phosphorus [TDP], soluble reactive phosphorus [SRP]), the concentration of nitrogen (total nitrogen [TN], dissolved inorganic nitrogen [DIN], nitrate-nitrogen [NO_3^-], ammonium-nitrogen [NH_4^+]), the concentration of dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC), the concentration of bicarbonate, anions (chloride [Cl], sulfate [SO_4]), and cations (sodium [Na], potassium [K], calcium [Ca],

magnesium [Mg], iron [Fe], silica [Si]), pH, conductivity, and alkalinity. All chemical analyses were measured in the University of Alberta limnology laboratory using the techniques described in Bayley and Prather (2003). The biological factors measured included Chl *a* concentrations (as a proxy for algal biomass) and percent cover of SAV. Chl *a* samples were filtered onto Gelman A/E filters within 24 h of collection. Chl *a* was extracted in 95% ethanol and analyzed with a spectrophotometer at 750, 665, and 649 nm following the methods of Bergmann and Peters (1980). SAV was estimated using a ranked scale of percent cover that ranged from 1 to 5, where: S1 = no plant cover; S2 = rare plant cover (<5%); S3 = occasional plant cover (5–25%); S4 = common plant cover (25–75%); and S5 = abundant plant cover (>75%) (Bayley and Prather 2003). The ranking included only SAV and excluded floating and emergent macrophytes. Both ranks and dry weight biomass of SAV were estimated and compared in the 24-lake subset. A significant correlation between SAV ranks and SAV biomass in the intensively monitored lakes (Pearson $r = 0.77$, $p < 0.001$, $n = 24$) indicated that SAV ranks provided a reasonable (and practical) surrogate for SAV biomass in lakes.

Lake characteristics based on remotely sensed measurements—Satellite-based estimates of Chl *a* (*satChl a*) were collected from 1984 to 2003 (1992 and 1996 were omitted due to high cloud cover). Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM) satellite images were selected from the archives that satisfied the following criteria: (1) the image captured the summer algal biomass (late July or August), (2) the image coincided with the timing of the ground-based estimates of Chl *a*, and (3) the image had no or minimal cloud. Landsat TM band three images (0.63–0.69 μm) were georectified using maps of streams, lakes, and roads, and then radiometrically normalized using a pseudo-invariant features-correction method (cf. Kloiber et al. 2002) creating images with normalized digital numbers (nDN) at 25-m pixel resolution. A 3×3 window (9 pixels) at the center of each lake was used to extract an average nDN from the satellite-based sample of Chl *a*. Some lakes were excluded from this analysis: (1) lakes with area less than 100 pixels (~0.05 km²) were excluded to avoid errors resulting from “mixed” pixels that combined lake and shoreline; (2) lakes with a standard deviation in Landsat TM band 5 less than 2.0 were excluded to avoid errors resulting from “mixed” pixels that combined open water and water with emergent and floating aquatic vegetation (water is a strong absorber of radiation in Landsat TM band 5 (1.55–1.75 μm), and therefore water alone would have a small standard deviation); (3) lakes with cloud cover for a given year were excluded from the spatial analysis of alternative states; and (4) lakes with cloud cover in any of the years in the 1984–2003 period were excluded from the temporal analysis of the stability of alternative states. Linear regression analysis was used to relate log-transformed Chl *a* and nDN for images where the satellite overpass occurred within 2 d of the collection of Chl *a* data ($r^2 = 0.68$, $\text{SE} = 0.65$, $p < 0.0001$, $n = 18$) (Sass et al. 2007). The linear regression equation was used to convert nDN to *satChl a*.

A one-way analysis of variance (ANOVA) was conducted to test if Landsat TM band three was sensitive to Chl *a* in algae and SAV. The results indicated that nDN was sensitive to changes in Chl *a* in algae but not SAV ($F = 0.62$, $p = 0.66$, $n = 18$). Therefore, *satChl a* was indicative of Chl *a* in algae only.

Clear versus turbid lakes—The concept of clear or turbid state in a lake is a visual one determined by an observer. To relate the clear or turbid status to algal biomass (as Chl *a*), several approaches were used.

A visual assessment of clarity was made from a boat (or helicopter) on each lake sampled from 2001–2005 ($n = 112$). The visual assessment was conducted the same day as Chl *a* assessment. If the observer was able to see the lake bottom and/or see deep into the SAV, the lake was classified as “clear.” If the observer was unable to see the lake bottom, or only the surface of the SAV or observed algal blooms, the lake was classified as “turbid.”

A cluster analysis was used to identify the threshold in Chl *a* for defining clear versus turbid lakes. A K-means clustering algorithm was used, which iteratively placed each sample into a homogeneous cluster until each cluster had a center that was the mean position of all the samples in that cluster and each sample was in the cluster with a center it was closest to. The K-means clustering algorithm was used on each lake sampled from 2001–2005 ($n = 112$) to identify the threshold in Chl *a* below which lakes were defined as clear and above which lakes were defined as turbid.

A nonmetric multidimensional scaling (NMDS) was used to graphically illustrate how clear and turbid lakes were arranged along physical, chemical, and/or biological gradients. NMDS is a multivariate ordination technique that is effective at summarizing and arranging sites along environmental gradients (McCune and Grace 2002). An environmental matrix of 97 sites (2001 data only) and 12 environmental factors was used for this analysis. The Sørensen (Bray-Curtis) distance measure was used, and the data were relativized for this analysis (McCune and Grace 2002). Multivariate analysis was conducted using PC-Ord v.4.25 software (MjM Software Design).

Evidence of alternative stable states?—Scheffer and Carpenter (2003) suggested three approaches that can be used as evidence for the existence of alternative stable states. We explored these three lines of evidence in our lakes: (1) an analysis of Chl *a* in each lake from 2000–2005 that focused on detecting jumps in time series of Chl *a* in each lake (all lakes were analyzed, but data from four different lakes are presented in the results to illustrate the main patterns); (2) an analysis of Chl *a* in all lakes from 2000–2005 that focused on identifying multimodality in the frequency distribution of Chl *a*; and (3) tests for dual relationships of Chl *a* in relation to limiting factors (i.e., TP) (cf. Scheffer and Carpenter 2003).

Controls on alternative vegetative regimes—Prior to statistical analyses, data were tested for the assumptions of normality and constant variance. Simple linear re-

gression analyses were conducted to relate TP to Chl *a* across different SAV ratings. Analysis of covariance (ANCOVA) was conducted to determine whether regression slopes among SAV ratings in each simple linear regression analysis were significantly different (Zar 1996). All regression analyses were performed using SPSS software (SPSS Inc.).

Stability versus instability of alternative vegetative regimes—To assess if the vegetative regime was “stable” in these lakes, we characterized the yearly summer Chl *a* in the intensively studied lakes (and in the remotely sensed lakes). As stated in the methods, SAV in these lakes rarely persists from year to year. With the long ice-covered season and anoxic conditions, vegetation and probably other organisms are “reset” each year. A stable state was defined as one that remained in the same vegetative state for more than one summer. If either the ground or satellite-based Chl *a* remained below or above the $18 \mu\text{g Chl } a \text{ L}^{-1}$ critical threshold from one summer to the next summer, the lake was considered stable. If, however, Chl *a* changed from $<18 \mu\text{g Chl } a \text{ L}^{-1}$ to $>18 \mu\text{g Chl } a \text{ L}^{-1}$ or vice versa, then the lake was considered unstable and a “switch” had occurred (data supporting the $18 \mu\text{g Chl } a \text{ L}^{-1}$ threshold is presented below). In this analysis, we used only those lakes with complete data coverage. We counted the number of switches for each lake during the 20-yr study period (omitting 1992 and 1996 due to high cloud cover) to establish the frequency of switching. We counted the number of lakes with identical switching patterns to establish the degree to which lakes showed synchrony in switching.

Results

Clear versus turbid lakes—Clear and turbid lakes were defined by Chl *a* concentration measured during the summer. Cluster analysis (a K-means clustering algorithm) identified a threshold in the concentration of Chl *a* of $18 \mu\text{g L}^{-1}$ to define alternative states; lakes with $<18 \mu\text{g Chl } a \text{ L}^{-1}$ were clear, and lakes with a $>18 \mu\text{g Chl } a \text{ L}^{-1}$ were classified as turbid (Fig. 2). Support for the $18 \mu\text{g Chl } a \text{ L}^{-1}$ threshold was provided by lakes classifications based on thresholds ranging from 5 to $30 \mu\text{g Chl } a \text{ L}^{-1}$ and then by assessments of the accuracy of each set of classified lakes calculated by the proportion of correctly classified lakes as determined by visual inspection of each lake at the time the lake was sampled. The threshold of $18 \mu\text{g Chl } a \text{ L}^{-1}$ resulted in correct classification of 86% of the lakes as clear or turbid based on visual observation.

Use of the $18 \mu\text{g Chl } a \text{ L}^{-1}$ threshold also resulted in statistically significant differences in the physical, chemical, and biological properties of clear and turbid lakes (Table 1). Clear lakes were relatively nutrient poor, with significantly lower concentrations of phosphorus (i.e., TP, TDP, and SRP), nitrogen (i.e., TN), and carbon (i.e., DOC) ($p < 0.05$) compared to turbid lakes. In contrast, NH_4 and NO_3 were lower, but not significantly lower, suggesting that other forms were driving the statistically significant differences in TN. Silica, important in the formation of

Table 1. Median values for physical, chemical, and biological parameters in clear and turbid lakes sampled during the 2001 synoptic survey ($n = 97$); p values are from Mann-Whitney U tests.

	Units	Clear ($<18 \mu\text{g L}^{-1}$ Chl a)	Turbid ($\geq 18 \mu\text{g L}^{-1}$ Chl a)	p value
<i>Physical factors</i>				
Maximum depth	cm	109	105	0.52
Secchi depth	cm	100	60	0.00
Turbidity	NTU	0.91	2.9	0.00
Secchi depth : maximum depth	ratio	1.0	0.6	0.00
<i>Chemical factors</i>				
Total phosphorus (TP)	$\mu\text{g L}^{-1}$	39.2	122.5	0.00
Total dissolved phosphorus	$\mu\text{g L}^{-1}$	18.3	31.7	0.00
Soluble reactive phosphorus (SRP)	$\mu\text{g L}^{-1}$	3	10.2	0.00
Total nitrogen (TN)	$\mu\text{g L}^{-1}$	1,874	3,193	0.01
Ammonium ($\text{NH}_4^+ - \text{N}$)	$\mu\text{g L}^{-1}$	20.1	18.7	0.56
Nitrate ($\text{NO}_3^- - \text{N}$)	$\mu\text{g L}^{-1}$	7.0	8.8	0.26
TN : TP	ratio	43.4	22.4	0.00
($\text{NH}_4^+ + \text{NO}_3^-$) : SRP	ratio	6.6	2.9	0.02
Dissolved organic carbon	mg L^{-1}	33.3	45.0	0.04
Dissolved inorganic carbon	mg L^{-1}	17.2	11.2	0.04
pH		8.3	8.3	0.93
Conductivity	$\mu\text{S cm}^{-1}$	180.0	180.7	0.62
Alkalinity	mg L^{-1}	79.0	67.9	0.12
Bicarbonate	mg L^{-1}	83.5	67.2	0.08
Chloride	mg L^{-1}	0.2	0.2	0.61
Sulfate	mg L^{-1}	7.8	8.8	0.45
Sodium	mg L^{-1}	3.0	2.9	0.82
Potassium	mg L^{-1}	2.1	1.9	0.52
Calcium	mg L^{-1}	25.0	23.3	0.45
Magnesium	mg L^{-1}	7.3	7.0	0.46
Iron	mg L^{-1}	0.1	0.1	0.57
Silica	mg L^{-1}	0.7	2.2	0.00
<i>Biological factors</i>				
Chlorophyll a	$\mu\text{g L}^{-1}$	5.6	32.1	0.00
Submersed aquatic vegetation	rating	4	3	0.00

Controls on alternative vegetative regimes—In the 97 lakes sampled in the 2001 synoptic survey, TP showed strong control on Chl a ; however, the presence of SAV modified the relationship between TP and Chl a (Fig. 6). As the abundance of SAV increased, the relationship between TP and Chl a differed significantly (Fig. 6). The increasing abundance of SAV weakened the positive relationship between TP and Chl a (ANCOVA: $F_{3,89} = 11.74$, $p < 0.05$), suggesting that the threshold in the concentration of TP for the transition from a clear to a turbid state was probably higher in lakes with high SAV. There was no statistically significant relationship between TP and Chl a when SAV covered more than 75% of the lake (Fig. 6).

For intensive study lakes sampled from 2001–2005, TP also showed a strong control of Chl a for lakes with low SAV cover (Fig. 7). The year-to-year fluctuations in the average TP of the lakes were mirrored in Chl a , but only in lakes with low SAV cover ($<5\%$). When the average TP was $>50 \mu\text{g L}^{-1}$, the majority of lakes were turbid. In contrast, when the average TP was $<50 \mu\text{g L}^{-1}$, the majority of lakes were clear. The average TP may need to be substantially $>100 \mu\text{g L}^{-1}$ before lakes with medium or high SAV cover change from clear to turbid states (Fig. 7).

Stability versus instability of alternative vegetative regimes—Ground- versus satellite-based estimates of alternative states: There was strong similarity in the classification of alternative states for ground- versus satellite-based methods for lakes sampled from 2001–2003 (cloud cover precluded analysis of lakes in 2004 and 2005). Ground-based methods estimated that 66.7% of lakes were clear and 33.3% of lakes were turbid (16 vs. 8 lakes, respectively), while satellite-based methods estimated that 70.8% of lakes were clear and 29.2% of lakes were turbid (17 vs. 7 lakes, respectively). There was also strong similarity in the degree of switching between alternative states for ground- versus satellite-based methods. Both ground- and satellite-based monitoring of lakes indicated that 28.6% remained stable (all clear) and 71.4% switched (57.1% switched once, and 14.3% switched twice) (Table 2).

Satellite-based analysis of stability of alternative states: The majority of lakes were clear in any given year based on analysis of lakes over a 20-yr period (Table 3). However, individual lakes did not necessarily remain clear (or turbid) the following year, and there was some synchronicity in switching from clear to turbid or vice versa among lakes in the landscape. For lakes surveyed from 1984–2003 ($n = 82$), the number of lakes that were stable for the entire period

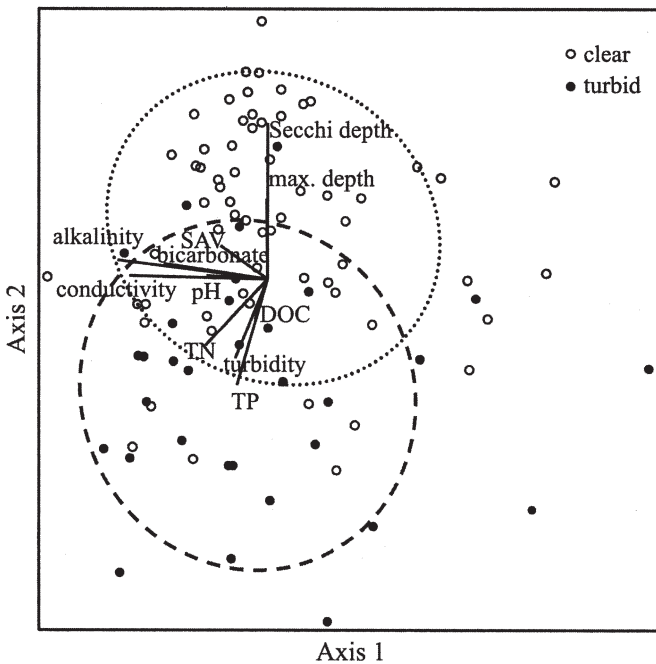


Fig. 3. The joint plot of NMDS ordination for clear and turbid lakes sampled during the 2001 synoptic survey ($n = 97$). Environmental vectors with $r^2 > 0.20$ are shown overlaying the plot (final stability = 12.0, 75 iterations). The three axes accounted for 90.5% of the variance in the data set, with 44.6% on the first axis, 27.7% on the second axis, and 18.3% on the third axis. Axis three is not shown.

was only 20.7%, with all of them remaining clear ($n = 17$). Of the remaining lakes, 7.3% switched once, 12.2% switched twice, and more than 60% switched at least three times (Table 3). Among the unstable lakes, there was synchronicity in the switching between alternative states (Table 4). In any given year, on average, 23% of lakes switched from one year to the next (Table 4).

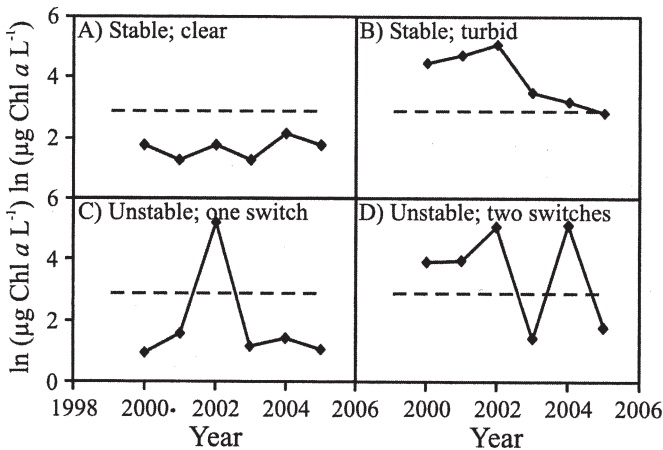


Fig. 4. Time series of $\ln(\text{Chl } a)$ for lakes exhibiting different states: (A) stable clear, (B) stable turbid, (C) unstable with one switch, and (D) unstable with multiple switches. Each panel shows an example of one lake in each category.

Table 2. Comparison of stability derived using ground-based and satellite-based methods for the intensively monitored lakes from 2001–2003 ($n = 7$ for each of 3 yr; satellite data for 2004 and 2005 were not available due to high cloud cover).

State	Ground-based estimates		Satellite-based estimates	
	Lakes (No.)	Lakes (%)	Lakes (No.)	Lakes (%)
Stable clear	2	28.6	2	28.6
Stable turbid	0	0.0	0	0.0
1 switch	4	57.1	4	57.1
2 switches	1	14.3	1	14.3

Table 3. Number of switches in alternative states in 82 lakes monitored from 1984 to 2003 (1992 and 1996 omitted due to high cloud cover).

	Lakes (No.)	Lakes (%)
Stable clear	17	20.7
Stable turbid	0	0.0
1 switch	6	7.3
2 switches	10	12.2
3 switches	6	7.3
4 switches	17	20.7
5 switches	6	7.3
6 switches	10	12.2
7 switches	3	3.7
8 switches	3	3.7
9 switches	4	4.9

Discussion

The majority of shallow lakes on the western Boreal Plain in central Alberta are clear in any given year. Both ground- and satellite-based measurements showed that ~70% of the lakes were clear in any one year. This should not be surprising given that the lakes and landscape in this region are generally unaffected by human activity. There

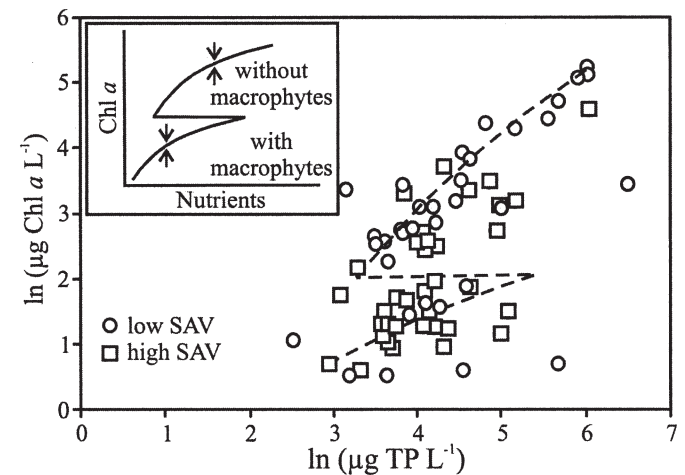


Fig. 5. Dual relationship between TP and $\text{Chl } a$ for lakes with low (<5% cover) and high (>25% cover) SAV based on 2001–2005 data set. Inset figure based on conceptual model of Scheffer et al. (2001). The lines in our data were drawn by eye.

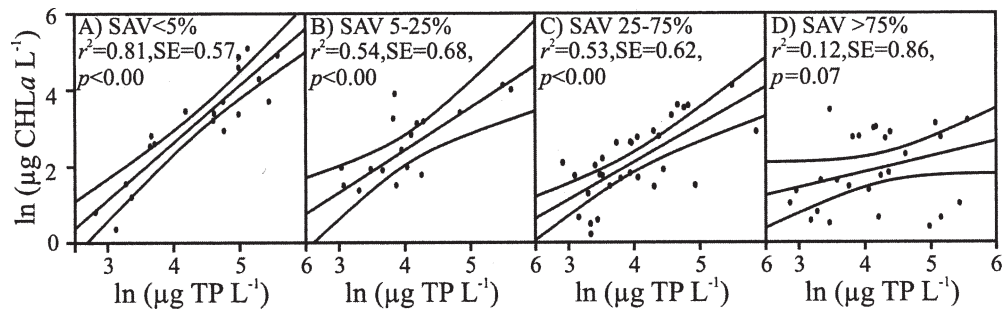


Fig. 6. Effects of SAV cover on the relationship between TP ($\mu\text{g L}^{-1}$) and Chl *a* ($\mu\text{g L}^{-1}$) in lakes sampled during the 2001 synoptic survey: (A) SAV cover $<5\%$, (B) SAV cover 5–25%, (C) SAV cover 25–75%, and (D) SAV cover $>75\%$. The regression equations for the different SAV cover classes are: (A) $y = \ln(1.30x) - 2.80$, (B) $y = \ln(1.01x) - 1.51$, (C) $y = \ln(0.86x) - 1.18$, and (D) $y = \ln(0.36x) + 0.59$.

are few human settlements, no agriculture, and limited forestry, although the region has roads and seismic lines associated with drilling and extraction of oil and gas. Therefore, our findings that $\sim 70\%$ of the lakes were clear supports the supposition by Scheffer (1998) that prior to human development, most shallow lakes were in a clear state.

Do alternative vegetative regimes exist in the lakes?—Visually, most lakes are in either a clear or turbid condition. The Chl *a* threshold above which lakes appear turbid is $\sim 18 \mu\text{g Chl } a \text{ L}^{-1}$; a similar threshold was also found by Zimmer (pers. comm.) in Minnesota lakes. Most lakes have Chl *a* concentrations between $3 \mu\text{g L}^{-1}$ and $17 \mu\text{g L}^{-1}$, and most of those have high densities of SAV. The predominance of this SAV-dominated regime does not imply that the lakes are not dynamic. The lakes can exhibit a multiplicity of states or vegetative regimes. For example, 14% of lakes in the synoptic survey have high Chl

a concentrations and still retain high densities of SAV (such sites would be classified as turbid since Chl *a* concentrations exceed $18 \mu\text{g Chl } a \text{ L}^{-1}$). The algal communities are also diverse (Norlin et al. 2005a,b) and can fluctuate widely through the growing season. However by the midsummer, most lakes are dominated by either algae or by SAV and hence seem to exhibit alternative vegetative regimes or states.

There have been a number of reviews that have synthesized the literature on alternative stable states in ecological systems and identified the difficulties of conclusively demonstrating alternative stable states in nature (e.g., Scheffer and Carpenter 2003; Schröder et al. 2005). Given that the biotic communities in lakes are never stable, in the sense that they always fluctuate, Scheffer and Carpenter (2003) suggested that the term “alternative stable states” be replaced with “alternative regimes” or “alternative attractors,” which acknowledge the dynamic nature of natural environments. While alternative stable states are never

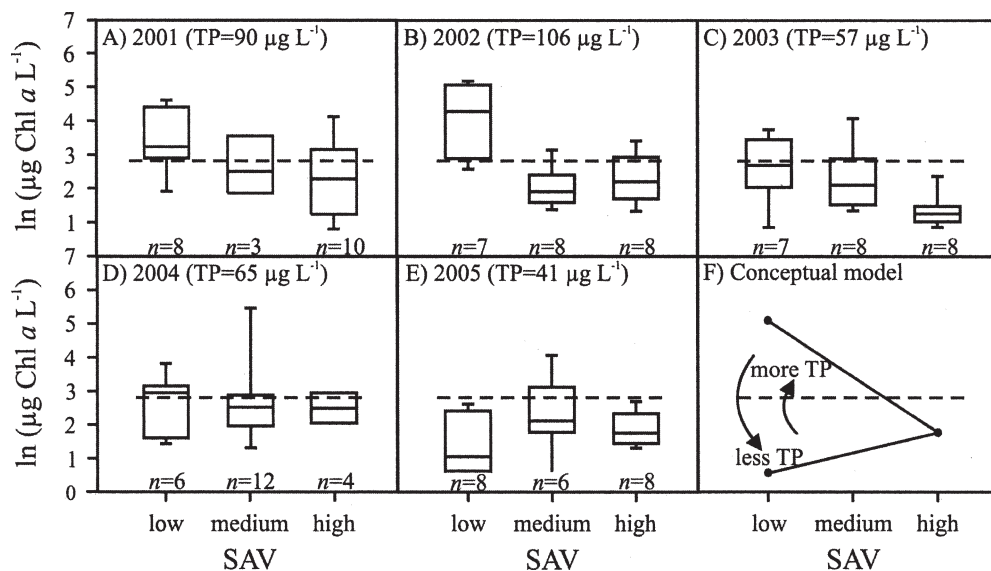


Fig. 7. Box plots of Chl *a* for three main SAV categories for each year from 2001 to 2005. Low SAV cover is S1 + 2, which is $<5\%$. Medium SAV cover is S3, which is 5–25%. High SAV cover is S4 + 5, which is $>25\%$. Dashed line represents $18 \mu\text{g Chl } a \text{ L}^{-1}$ clear/turbid threshold. TP values represent the average of all lakes for a given year.

Table 4. Synchronicity of switches between alternative states in the lakes in the study area from 1984 to 2003 ($n = 82$; 1992 and 1996 omitted due to high cloud cover).

Year	Turbid (%)	Clear (%)	Switch (%)	Switched to turbid (%)	Switched to clear (%)
1984	19.5	80.5	na	na	na
1985	43.9	56.1	36.6	30.5	6.1
1986	34.1	65.9	24.4	7.3	17.1
1987	31.7	68.3	26.8	12.2	14.6
1988	45.1	54.9	23.2	18.3	4.9
1989	39.0	61.0	18.3	6.1	12.2
1990	30.5	69.5	28.0	9.8	18.3
1991	24.4	75.6	20.7	7.3	13.4
1992	na	na	na	na	na
1993	40.2	59.8	na	na	na
1994	36.6	63.4	18.3	7.3	11.0
1995	22.0	78.0	22.0	3.7	18.3
1996	na	na	na	na	na
1997	23.2	76.8	na	na	na
1998	43.9	56.1	28.0	24.4	3.7
1999	32.9	67.1	20.7	4.9	15.9
2000	17.1	82.9	28.0	6.1	22.0
2001	28.0	72.0	20.7	15.9	4.9
2002	23.2	76.8	14.6	4.9	9.8
2003	18.3	81.7	14.6	4.9	9.8
Avg.	30.8	69.2	23.0	10.9	12.1

truly stable, Scheffer and Carpenter (2003) suggested some lines of evidence that would help confirm the existence of alternative stable states in ecosystems. These lines of evidence include abrupt shifts in states, bimodality in the frequency distribution of states, and dual relationships to a control factor. Our analyses of these three lines of evidence (*see* Results) suggest that our lakes generally did not exhibit alternative stable states. The most important evidence is the time-series analysis, which shows that most lakes jump from a clear state to a turbid state but seldom remain in a turbid state for more than a few years before returning to the clear state. The other two lines of evidence are inconclusive and could suggest alternative stable states if the time-series analysis showed that the lakes persisted in a new state. We only observed a weak bimodality in our Chl *a* concentrations (Fig. 2), and as noted by Scheffer and Carpenter (2003), even a strong bimodal pattern does not necessarily imply alternative attractors. Similarly we found a dual relationship between TP (the primary control factor) and Chl *a* (Fig. 5), which again could offer partial support for the existence of alternative stable states. Later, we will discuss how the mechanisms that are important in more temperate climates to maintain the vegetative regimes in one state or the other may be weakened by winter conditions under ice.

How stable are alternative vegetative regimes in the lakes?—The majority of lakes are clear in any given year, but many of these lakes are unstable, frequently switching from clear to turbid and back to clear again. Both ground- and satellite-based data sets showed that these lakes are highly unstable. Ground-based measurement of seven lakes over 3 yr showed that ~70% switched

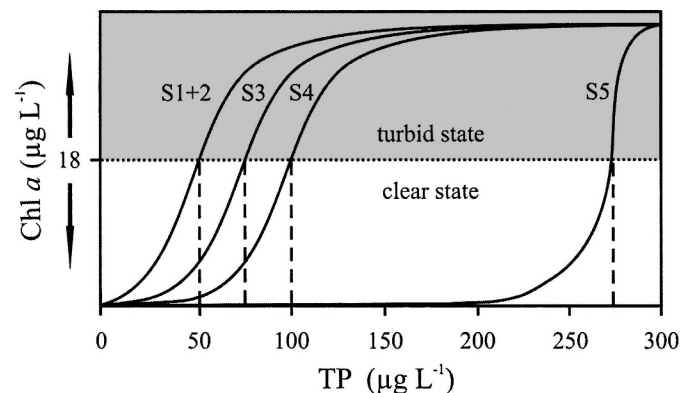


Fig. 8. Schematic diagram of the effect of SAV abundance on the relationship between concentration of total phosphorus and Chl *a* (clear vs. turbid state) in a given lake. The sigmoid solid lines represent different SAV densities (S1 + 2 is <5% cover; S3 is 5–25% cover; S4 is 25–75% cover, and S5 is >75% cover). The dashed lines show the point at which the SAV curves intersect the 18 $\mu\text{g Chl } a \text{ L}^{-1}$ threshold for clear versus turbid state. The intercept point is the approximate TP.

states (Table 2). Satellite-based monitoring of 82 lakes over 20 yr showed that over 60% switched at least three times (Table 3). Only 20% of the 82 lakes remained in one state for the 20-yr period. No lakes stayed turbid for the entire period. On average, 23% of lakes switched each year (Table 4). Lakes switched states somewhat in synchrony (Table 4), although we cannot speculate why at this time.

What controls alternative vegetative regimes?—Phosphorus is clearly an important factor affecting Chl *a* concentrations, as has been shown in many lakes around the world (Schindler 1978), and it is directly related to the turbidity of shallow lakes in many regions (Scheffer 1998; Bayley and Prather 2003). Most of the lakes in this region ranged from 25 $\mu\text{g TP L}^{-1}$ to 100 $\mu\text{g TP L}^{-1}$, which is the range of concentrations of TP where lakes are most likely to switch from one alternative state to another (Scheffer and Jeppesen 1998). However, the concentration of TP predicted only 40% of the variance in concentration of Chl *a* in the synoptic lake survey ($n = 97$, $r^2 = 0.40$, $\text{SE} = 0.84$, $p < 0.00$). We found that the TP versus Chl *a* relationship was affected by SAV cover (Fig. 6). The threshold in TP beyond which a lake shifted from a clear to a turbid state was modified by the percentage cover of SAV in the lake. The schematic shown in Fig. 8 was developed from a three-dimensional bar plot of TP, Chl *a*, and SAV cover for the 97 lakes of the synoptic survey, which was then adapted to a two-dimensional schematic. The TP threshold for lakes with no to little SAV cover (S1 + S2) shifts to a turbid state at ~50 $\mu\text{g TP L}^{-1}$. In lakes with SAV cover in the range 5–25% (S3), the TP threshold is 75 $\mu\text{g TP L}^{-1}$. In lakes with SAV cover in the range 25–75% (S4), the TP threshold is 100 $\mu\text{g TP L}^{-1}$. In lakes with a dense SAV cover >75% (S5), the threshold is ~275 $\mu\text{g TP L}^{-1}$. Thus, the concentrations of TP associated with a shift in alternative state in many shallow lakes (50–150 $\mu\text{g TP L}^{-1}$; Scheffer 1998) are appropriate only for lakes with little or lower amounts of SAV. Once a substantial SAV cover has

become established, lakes can tolerate much higher concentrations of TP without shifting to a turbid state, as has been noted by others (Beklioglu and Moss 1996; Bachmann et al. 2002).

The combination of TP and SAV is an important control on alternative vegetative regimes in our lakes. However, the question remains: what drives the temporal variations in either TP or SAV? Large “catastrophic” perturbations (such as major floods) are often considered important in terms of driving a switch between alternative states (Scheffer et al. 1993, 2001). However, smaller perturbations may also be important in driving a switch between alternative states if the processes that maintain the clear (or turbid) state are weak (i.e., the lakes lack resilience) (Scheffer et al. 2001; Genkai-Kato and Carpenter 2005). Given the frequency of switching of states, we suspect that the alternative states in our lakes are maintained by weak processes and that small perturbations can displace them from one to another state.

The processes that cause the regime shifts in these lakes are unknown, but we suspect that they are associated with the emergence of SAV. One important question is: given the shallow depth of lakes, why does SAV cover not establish every year and support the processes that make lakes clear? At shallow depths, light can penetrate to the bottom of the lakes and therefore foster the establishment and growth of submersed macrophytes (Chambers and Kalff 1985). Lakes in this region were generally extremely shallow (average maximum depth of 1.26 m, range 0.30–3.20 m). Given the shallowness of lake depths, we would expect all lakes in the region to support substantial cover of SAV. While many lakes did have substantial SAV cover, some did not. Approximately 10% of lakes had no SAV cover, and 40% of lakes had less than 25% SAV cover.

In this region, harsh winter conditions cause plant senescence each autumn, and spring conditions become crucial for the “re”-establishment and growth of SAV. Several physical and climatic factors may directly affect the emergence of SAV. First, cold conditions may delay growth of SAV in the early spring. Second, anoxic conditions in soils in the contributing catchment area may result in large loading of TP to the open waters, which would favor algal growth in the early spring (Søndergaard et al. 2003). Third, windy conditions may result in resuspension of the TP-rich sediments into the open waters, which would favor algal growth in the early spring (many of our study lakes had TP in sediments $>1 \text{ mg m}^{-2}$; unpubl. data). Fourth, water levels in the early spring may exceed the 1.75 m necessary for light penetration in these high-DOC systems. Therefore, SAV growth may be delayed until summer evaporation reduces water levels, thereby favoring algal growth in the early spring. Finally, SAV diversity in these shallow lakes is low (unpubl. data), and this enhances the probability that one or two important species could be affected by weather conditions (Gonzalez Sangrario et al. 2005).

Our data support Didham et al.’s (2005) theory that strongly abiotic or disturbance-structured systems appear to be more prone to catastrophic regime shifts but not their suggestion that strongly abiotically regulated systems have alternative states that are more stable over time. The harsh

winter conditions appear to diminish the importance of trophic controls on algal biomass, which are dominant factors controlling the existence of alternative regimes in many other regions (e.g., Hanson and Riggs 1995; Zimmer et al. 2001, 2002). The winter climate “resets” not only SAV but also the macroinvertebrate, zooplankton, and fish communities. Many lakes freeze to the bottom, eliminating all fish (Conlon 2002; Tonn et al. 2004). Even those lakes that do not freeze to the bottom may have anoxic water conditions under the ice that eliminate or reduce the numbers of fish; the only fish present in most of these lakes is brook stickleback (*Culea inconstans*). In both cases, there is a fundamental loss or restructuring of species in the macroinvertebrate, zooplankton, and fish communities (Wellborn et al. 1996; Isermann et al. 2004; Norlin et al. 2005a). In our intensive study lakes, Norlin et al. (2005a) found that even the presence of fish does not necessarily result in the turbid state due to the reduction in fish numbers in early spring. Re-establishment of fish communities is problematic because most of the lakes are hydrologically isolated, receiving surface flow only in years of high precipitation, which typically may be every 15 yr or so (Devito et al. 2005; Sass 2006).

Given the harsh winter conditions in western boreal shallow lakes, many of the biotic communities are “reset” each year, and, hence, it is not surprising that our shallow lakes are unstable and lack resilience to switches between clear and turbid states. The lack of stability in these systems raises a number of interesting questions about their ability to tolerate additional nutrient loading from human activities such as agriculture, logging, or residential developments. Presumably they would be highly susceptible to additional phosphorus, and more lakes would become turbid and would remain turbid.

References

- BACHMANN, R. W., C. A. HORSBURGH, M. V. HOYER, L. K. MATARAZA, AND D. E. CANFIELD, JR. 2002. Relations between trophic state indicators and plant biomass in Florida lakes. *Hydrobiologia* **470**: 219–234.
- BAYLEY, S. E., AND C. M. PRATHER. 2003. Do wetland lakes exhibit alternative stable states? Submersed aquatic vegetation and chlorophyll in western boreal shallow lakes. *Limnol. Oceanogr.* **48**: 2335–2345.
- BEISNER, B. E., D. T. HAYDON, AND K. CUDDINGTON. 2003. Alternative stable states in ecology. *Front. Ecol. Environ.* **1**: 376–382.
- BEKLIÖGLU, M., AND B. MOSS. 1996. Existence of a macrophyte-dominated clear water state over a very wide range of nutrient concentrations in a small shallow lake. *Hydrobiologia* **337**: 93–106.
- BERGMANN, M., AND R. H. PETERS. 1980. A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus-chlorophyll-seston relationship. *Can. J. Fish. Aquat. Sci.* **37**: 111–114.
- BLINDOW, I. 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. *Freshwater Biol.* **28**: 15–27.
- , G. ANDERSSON, A. HARGEBY, AND S. JOHANSSON. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshwater Biol.* **30**: 159–167.

- CARPENTER, S. R., AND D. M. LODGE. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquat. Bot.* **26**: 341–370.
- , D. LUDWIG, AND W. A. BROCK. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* **9**: 751–771.
- CHAMBERS, P. A., AND J. KALFF. 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. *Can. J. Fish. Aquat. Sci.* **42**: 701–709.
- CONLON, M. R. 2002. Predicting fish assemblages in small, boreal lakes in Alberta using landscape and local factors. M.Sc. thesis, Univ. of Alberta.
- DEVITO, K. J., I. F. CREED, AND C. J. D. FRASER. 2005. Controls on runoff from a partially harvested aspen-forested head-water catchment, Boreal Plain, Canada. *Hydrol. Process.* **19**: 3–25.
- DIDHAM, R. K., C. H. WATTS, AND D. A. NORTON. 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? *Oikos* **110**: 409–416.
- GENKAI-KATO, M., AND S. R. CARPENTER. 2005. Eutrophication due to phosphorus recycling in relation to lake morphometry, temperature, and macrophytes. *Ecology* **86**: 210–219.
- GILES, N. 1987. Differences in the ecology of wet-dug and dry-dug gravel pit lakes. *Game Conserv. Ann. Rev.* **18**: 130–133.
- GONZALEZ SAGRARIO, M. A., E. JEPPESEN, J. GOMA, M. SØNDERGAARD, J. P. JENSEN, T. LAURIDSEN, AND F. LANDKILDEHUS. 2005. Does high nitrogen loading prevent clear-water conditions in shallow lakes at moderately high phosphorus concentrations? *Freshwater Biol.* **50**: 27–41.
- HANSON, M. A., AND M. R. RIGGS. 1995. Potential effects of fish predation on wetland invertebrates—a comparison of wetlands with and without fathead minnows. *Wetlands* **15**: 167–175.
- HARGEBY, A., G. ANDERSSON, I. BLINDOW, AND S. JOHANSSON. 1994. Trophic web structure in a shallow eutrophic lake during a dominance shift from phytoplankton to submersed macrophytes. *Hydrobiologia* **279/280**: 83–90.
- ISERMANN, D. A., S. R. CHIPPS, AND M. L. BROWN. 2004. Seasonal *Daphnia* biomass in winterkill and nonwinterkill glacial lakes of South Dakota. *N. Am. J. Fish. Mana.* **24**: 287–292.
- JEPPESEN, E., AND OTHERS. 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: A study of 466 lakes from the temperate zone to the arctic. *Ecosystems* **6**: 313–325.
- KLOIBER, S. M., P. L. BREZONIK, L. G. OLMANSON, AND M. E. BAUER. 2002. A procedure for regional lake water clarity assessment using Landsat multispectral data. *Remote Sens. Environ.* **82**: 38–47.
- MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities. MjM Software Design.
- MOSS, B., S. MCGOWAN, AND L. CARVALHO. 1994. Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. *Limnol. Oceanogr.* **39**: 1020–1029.
- NOGES, P., AND OTHERS. 2003. Factors controlling hydrochemical and trophic state variables in 86 shallow lakes in Europe. *Hydrobiologia* **506**: 51–58.
- NORLIN, J. I., S. E. BAYLEY, AND L. C. M. ROSS. 2005a. Submersed macrophytes, zooplankton and the pre-dominance of low-over high-chlorophyll states in western boreal shallow water wetlands. *Freshwater Biol.* **50**: 868–881.
- , ———, AND ———. 2005b. Zooplankton composition and ecology and western boreal shallow-water wetlands. *Hydrobiologia* **560**: 197–215.
- SASS, G. Z. 2006. Hydrologic controls on the trophic status of shallow lakes on the Boreal Plain. Ph.D. thesis, Univ. of Western Ontario.
- , I. F. CREED, S. E. BAYLEY, AND K. J. DEVITO. 2007. Understanding variation in trophic status of lakes on the Boreal Plain: A 20 year retrospective using Landsat TM imagery. *Remote Sens. Environ.* **109**: 127–141. (doi: 10.1016/j.rse.2006.12.010)
- SCHAEFFER, M. 1998. Ecology of shallow lakes. Chapman & Hall.
- , AND S. R. CARPENTER. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *TREE* **18**: 648–656.
- , ———, J. A. FOLEY, C. FOLKES, AND B. WALKER. 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591–596.
- , S. H. HOSPER, M.-L. MEIJER, B. MOSS, AND E. JEPPESEN. 1993. Alternative equilibria in shallow lakes. *TREE* **8**: 275–279.
- , AND E. JEPPESEN. 1998. Alternative stable states, p. 397–406. *In* E. Jeppesen, M. Søndergaard, M. Søndergaard and K. Christoffersen [eds.], The structuring role of submersed macrophytes in lakes. Springer-Verlag.
- SCHINDLER, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. *Limnol. Oceanogr.* **23**: 478–486.
- SCHRÖDER, A., L. PERSSON, AND A. M. DE ROOS. 2005. Direct experimental evidence for alternative stable states: A review. *Oikos* **110**: 3–19.
- SØNDERGAARD, M., J. P. JENSEN, AND E. JEPPESEN. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* **506–509**: 135–145.
- TAKAMURA, N., Y. KADONO, M. FUKUSHIMA, M. NAKAGAWA, AND B. KIM. 2003. Effects of aquatic macrophytes on water quality and phytoplankton communities in shallow lakes. *Ecol. Res.* **18**: 381–395.
- TONN, W. M., P. W. LANGLOIS, E. E. PREPAS, A. J. DANYLCHUK, AND S. M. BOSS. 2004. Winterkill cascade: Indirect effects of a natural disturbance on littoral macroinvertebrates in boreal lakes. *J. Am. Benthol. Soc.* **23**: 237–250.
- WELLBORN, G. A., D. K. SKELLY, AND E. E. WERNER. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.* **27**: 337–363.
- ZAR, J. H. 1996. Biostatistical analysis. Prentice Hall.
- ZIMMER, K. D., M. A. HANSON, AND M. G. BUTLER. 2001. Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. *Ecosystems* **4**: 346–357.
- , ———, AND ———. 2002. Effects of fathead minnows and restoration on prairie wetland ecosystems. *Freshwater Biol.* **47**: 2071–2086.

Received: 14 July 2006

Accepted: 13 March 2007

Amended: 02 May 2007