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Do wetland lakes exhibit alternative stable states? Submersed aquatic vegetation and chlorophyll in western boreal shallow lakes

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Abstract

Shallow lakes often exhibit alternative vegetative states, one a clear-water state dominated by submersed aquatic vegetation (SAV) and the other a turbid state dominated by pelagic phytoplankton. We determined the nutrient and vegetation status of 148 wetland lakes in boreal Alberta, Canada. The lakes were very shallow (mean depth, 1.3 m), rich in phosphorus (123 μg total P L^{-1}), and relatively low in available nitrogen (18 μg L^{-1} $NH_4^+ + NO_3^-$), and 62% of them exhibited alternative states. The results of principal components analysis suggested that these lakes could be divided into four categories: (1) phytoplankton-dominated lakes (25%) with higher concentrations of chlorophyll *a* ($>$20 μg L^{-1}), are more turbid, and have low densities of SAV; (2) SAV-dominated lakes (37%), with high densities of submersed aquatic plants ($>$25% cover), are clearer, and have lower phytoplankton concentrations; (3) high SAV and high phytoplankton lakes (12%), with dense populations of both SAV and phytoplankton; and (4) low SAV and low phytoplankton lakes (26%), with low densities of both SAV and phytoplankton. The phytoplankton-dominated lakes are usually found in hypereutrophic conditions (mean = 205 μg TP L^{-1}), whereas the SAV-dominated lakes primarily exist in eutrophic and mesotrophic conditions (mean = 82 μg total P L^{-1}) and have lower available N (11 μg L^{-1} $NH_4^+ + NO_3^-$). Because most of these lakes lack fish, we expect that nutrient status, depth, and invertebrate predators are probably the most important determinants of vegetative structure and alternative states.

The boreal forest of Canada occupies 53% of the land surface and contains millions of lakes (Smith and Lee 2000). Given the abundance of lakes in the boreal ecoregion, surprisingly few surveys of their limnological properties have been made (Moser et al. 1998), and surveys of shallow lakes are especially rare. Shallow lakes ($<$2 m depth) in the western boreal forests of Canada are numerous and are often surrounded by wetland complexes. In Alberta, Saskatchewan, Manitoba, British Columbia, and the Northwest Territories, there are thousands of small wetland lakes embedded in fen/bog complexes or surrounded by marshes or upland forest. The vegetative community surrounding these small lakes is influenced by the topography and geology of the region. These shallow lake-wetland complexes (henceforth termed ‘‘shallow lakes’’) are increasingly recognized to be important to regional waterfowl populations. Studies of small wetland lakes are rare; most of the recent ecological work in western boreal wetlands has been in the emergent vegetation of the wetlands (Thormann and Bayley 1997) or in the larger lakes of the region (Prepas et al. 2001).

There has been some effort to characterize northern or boreal lakes in terms of their ability to support waterfowl, with the results of some studies suggesting that wetland productivity or ‘‘fertility’’ is important to water birds (Murphy et al. 1984). Lake productivity is often referred to in terms of chlorophyll *a* or total phosphorus (TP) concentrations (Wetzel 1983). Western boreal lakes in many areas are considered eutrophic to hypereutrophic with respect to TP (Prepas et al. 2001), although lakes located on the boreal shield or in karst geology are oligotrophic (Schindler 1978; Moser et al. 1998).

The primary productivity of the shallow lakes is characterized by mixed populations of phytoplankton and submersed aquatic vegetation (SAV) in the open water, and such lakes are often fringed by various species of emergent vegetation. Research in other parts of the world has indicated that the relative proportion of SAV and phytoplankton depends on nutrient loading, lake water depth, basin slope and size, and herbivory (Gasith and Hoyer 1998). Some shallow lakes appear to be dominated by SAV, whereas others appear to be dominated by dense phytoplankton blooms (and little SAV), a finding that has been labeled ‘‘alternative stable states’’ (Scheffer et al. 1993; Jeppesen et al. 1997). According to this theory, shallow lakes with intermediate to high TP concentrations can develop a stable state characterized by abundant SAV and clear water or an alternate state characterized by dense phytoplankton blooms and turbid water (Moss et al. 1994; Jeppesen et al. 1998). The growth of submersed aquatic macrophytes may be limited by lack of light due to high turbidity (from phytoplankton) (Gasith and Hoyer 1998), lack of light due to water depth (Moss et al. 1994), or low nitrogen (Carpenter et al. 1998).

Nutrient loading (bottom-up control), predatory fish and invertebrates (top-down control), climatic events (floods/droughts), or some combination of external and internal fac-

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tors may regulate these alternative states. In many European shallow lakes, the biotic control of phytoplankton is known to be important in determining the vegetation structure. Zooplankton control of phytoplankton may be related to fish population structure and presence (Søndergaard et al. 1990), especially in shallow lakes with frequent winter kill. In clear lakes, the SAV may act as a refuge for large-bodied *Daphnia* and piscivorous fish. Predation pressure by piscivores may reduce densities of planktivorous fish and thus release planktivorous predation on cladoceran grazers. Cladoceran grazers may control phytoplankton populations in the vegetated lakes (top-down control) (Jeppesen et al. 1997; Moss et al. 1998), enhancing the clear-water state. The SAV may create a refuge from planktivores for these grazers, positively influencing the clear-water state. In North America, the alternative states have been observed in prairie lakes, mostly in regions of intense agricultural activity (Schindler and Comita 1972; Zimmer et al. 2001).

A change in the abundance of fish has been credited with changing the trophic state of shallow lakes (e.g., Jeppesen et al. 2000; Zimmer et al. 2001). The role of fish can be particularly large in shallow lakes, because the biomass of fish per cubic meter of water is higher in shallow lakes than in deeper lakes (Jeppesen et al. 1997) and because they have access to alternative food resources that may facilitate the top-down control of zooplankton. Many western boreal lakes in Canada are shallow and freeze to the bottom in winter, and the smaller shallow lakes may lack fish (W. Tonn pers. comm.). Even the deeper lakes commonly have fish kills (Robinson and Tonn 1989; Conlon 2002; Danylchuk and Tonn pers. comm.). In our wetland lakes, control of the trophic status is unlikely to be related to fish, because most of the lakes experience winter-kill (and lack fish) (Danylchuk and Tonn pers. comm.; W. Tonn pers. comm.).

The purpose of the present study is to describe the trophic status of shallow lakes in the western boreal forest in relation to phytoplankton and SAV. The first objective is to characterize the patterns of SAV production and determine the importance of SAV relative to phytoplankton for the productivity of these shallow, boreal lakes. Second, we want to determine whether nutrients (especially TP or inorganic nitrogen) are related to vegetation abundance and water clarity. A unique feature of these lakes is their shallow depth (most are <1 m). Most of these boreal wetland lakes are even shallower than lakes studied in Europe or the North American prairie region. Keeping this in mind, the third objective is to determine whether there is evidence of alternative stable states under such shallow conditions.

Materials and methods

Description of the study area—The study area is located in north central Alberta, Canada (56°52′N, 115°27′W), in the Central Mixedwood Subregion of the Boreal Forest Natural Region. Most of the wetlands in this region are peat forming (>40 cm peat deposit) and include bogs, fens (open and tree-covered), swamps, and marshes. Human influence on these lakes is minimal. Deep glacial till covers the hill slopes and depressions, with little elevational relief between them. The soils are gray Luvisols and Brunisols in the uplands and organic deposits (peatlands) in the depressions. There are at least three landforms in the area: outwash plain (dominated by sands), moraine (with more depressions), and lacustrine plain (flat areas with clay and extensive peatlands). Our two study areas, each of which covered ~600 km^2, are located ~100 km apart (Utikuma and Mistehae areas), in north-central Alberta (Fig. 1). Although there are some differences in surficial geology and regional recharge and discharge (K. Devito pers. comm.), the three dominant landform types have been identified in both areas. Analysis of the chemistry of lake water from both areas showed that the chemistry of both areas is generally within the same range and there is no significant difference between the two areas in terms of phosphorus or Chl *a* concentrations, although the shallow lakes from Utikuma have denser amounts of SAV. Because one of our goals was to determine SAV abundance across a range of TP and Chl *a* concentrations, the shallow lakes from these two areas were combined into a single large data set. To ensure that the findings were not dictated by the regional differences between the two data sets, the data from each individual area (Utikuma and Mistehae) were analyzed separately and showed the same general patterns as the combined data set (seen in the later figures).

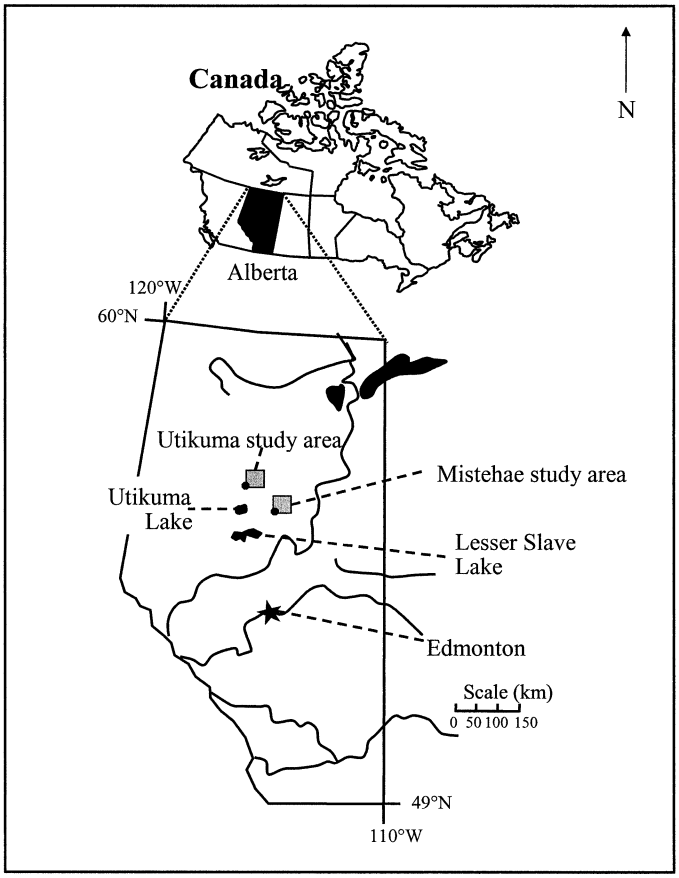

Fig. 1. Location of the Utikuma (55°57′N, 115°35′W) and Mistehae (55°45′N, 114°30′W) study areas in Alberta, Canada.

Helicopter survey—Two helicopter surveys were made in 1998; one in late June, when data on water-bird abundance, forest and wetland type, and submersed aquatic plant abundance were estimated; and one (in mid-August) in which a helicopter with floats was used to collect water samples from the center of the lakes. Initially, a total of 171 lakes, 93 from the Utikuma area and 78 from the Mistehae area in north-central Alberta, were sampled. The open water portion of the wetland lakes we sampled ranged in size from 0.02 to 0.50 km^2. The SAV cover, wetland type (marsh, bog, fen), and approximate extent of emergent wetland around the lakes and forest type (deciduous or coniferous) were also determined during these surveys. As with many large data sets, there was incomplete data collection for some sites, and a final total of 148 lakes were analyzed here (78 lakes in the Utikuma area and 70 lakes in the Mistehae area).

The relative cover and density of SAV were determined using a rating system that allowed comparison among these largely inaccessible lakes. The rating system integrated cover across the surface of the lake as well as the density of plants throughout the water column. This integrated cover and density rating will subsequently be referred to as ''SAV cover.'' Five rank categories were defined: (1) no plant cover observed (0%), (2) rare plant cover (<5%), (3) occasional plant cover (5%–25%), (4) common plant cover (25%–75%), and (5) abundant plant cover (>75%).

The ranking of relative cover included only submersed plants and excluded floating-leaved macrophytes, which were present in some sites but were not so dense that they obscured the visibility of the submersed vegetation. Because this was a helicopter survey, no identification of the submersed vegetation was done. However when water samples were collected, the most common species observed were *Potamogeton richardsonii* (Benn.) Rydb. (plus other *Potamogeton* species), *Myriophyllum exalbescens* Fern., and *Chara* species in some lakes.

Chemical analyses—Water samples were collected from the center of the open-water areas and analyzed for various chemical variables in the Limnology Laboratory, University of Alberta, including nitrogen (ammonia [NH_4^+], nitrate [NO_3^-], and total dissolved nitrogen [TDN]), phosphorus (soluble reactive phosphorus [SRP], total dissolved phosphorus [TDP], and TP), major ions (chloride, sulfate, sodium, potassium, calcium, magnesium, bicarbonate, and carbonate), and other components (dissolved organic carbon [DOC], color, turbidity, Chl *a*, alkalinity, conductivity, and pH). Total N was not measured.

Water samples for chemical analyses were prepared within 48 h. Water samples for NH_4^+-N were unfiltered, whereas samples for NO_3^--N were filtered using a 0.45-μm HAWP millipore filter (Vitt et al. 1995). SRP, TDP, and TP were analyzed according to the methods of Bierhuizen and Prepas (1985). Samples for chlorophyll analysis were filtered onto Gelman A/E filters within 24 h of collection. Chlorophyll was extracted in 95% ethanol and analyzed with a spectrophotometer at 750, 665, and 649 nm, according to the methods of Bergmann and Peters (1980).

The Chl *a* concentration was used as a proxy for phytoplankton biomass. The ratio of biologically available nitrogen (NH_4^+ and NO_3^-) to biologically available phosphorus (SRP) was calculated to provide an estimate of nutrient limitation (Redfield ratio). In the present article, only nutrient, Chl *a*, and vegetation data will be discussed.

Multivariate analysis—Principal components analysis (PCA), a type of gradient analysis or indirect ordination, is a statistical method that can be used on large, multivariate data sets. PCA is a recommended method for analysis of trends in environmental data, for which it is effective at drawing out complex, multivariate relationships among sites (Kent and Coker 1998). We considered it to be a good method to use on this data set to examine multivariate similarities between lakes based on water chemistry and vegetation. PCA is sensitive to outliers; thus, outlier analysis was run on the data prior to ordination analysis. The Sørensen percentage dissimilarity measure (run in the program SYSTAT version 10) is most useful for quantitative data and was used on this data set to determine outliers. Furthermore, data for each environmental parameter across the entire data set was standardized to a base of 100 (following Halsey et al. 1997) as a way to remove bias between variables with different ranges, means, and standard deviations. All ordination analyses were run in the program CANOCO for Windows (version 4.0) (ter Braak and Smilauer 1997). In the operation of the program, no sample weights were defined, the species data was log transformed, and scores were standardized by species. The ordination analyses were done on 148 lakes and 13 environmental pseudo species.

Backward stepwise multiple regression (in which one variable is removed at a time) was used to determine the variables that significantly influence the concentration of Chl *a* (phytoplankton) in shallow lakes. SYSTAT version 10 (SPSS) was used for the regressions. Two-Way SPecies INdicator ANalysis (TWINSPAN) in PC-ORD version 4.0 for windows (McCune and Mefford 1997) was used to objectively determine groups of shallow lakes. We transformed the environmental data into percentage values and used them as pseudo species. Cutoff values of 0%, 2%, 5%, 10%, 25%, and 50% were used to separate lakes into groups.

Grouping of lakes—Because we are interested in examining the primary producers within these shallow lakes, it seemed reasonable to separate the lakes into groups on the basis of the estimated abundance of both phytoplankton and SAV. We selected threshold values in both the Chl *a* data and the SAV cover data, to place a particular lake within a group. Lakes with <20 μg L^{-1} of Chl *a* were considered to have ''low'' phytoplankton, whereas those with >20 μg L^{-1} of Chl *a* were considered to have ''high'' phytoplankton. This value was partly based on the observation by Timms and Moss (1984) that lakes with <20 μg L^{-1} had very clear water conditions in shallow lakes and also on the bimodal distribution of Chl *a* concentrations observed in our study (see ''Results''). Likewise, lakes with 0%, <5%, and 5%–25% SAV cover were considered to have ''low'' cover, and lakes with >25% SAV cover were considered to have ''high'' cover. This threshold is also supported by the observation of Canfield et al. (1984) that at least 30% of the water volume needed to be occupied by macrophytes before

Table 1. Means (by study area) and overall ranges of water chemistry, Chl *a*, and submerged aquatic vegetation (SAV) abundance for the 148 lakes. The number of lakes in each group is given in parentheses. A non-parametric Mann-Whitney *U* test compared the two study sites.

Variable	Units	Utikuma (78)	Mistehae (70)	*P*	Minimum (148)	Maximum (148)	Mean of both sites (148)
Chl *a*	μg L^{-1}	29.6	40.4	0.290	0.9	343.6	34.1
SAV abundance	Rank	3.4	2.7	0.007**	1.0	5.0	3.1
TP	μg L^{-1}	112.1	137.0	0.229	15.7	726.6	123.2
TDP	μg L^{-1}	49.0	73.5	0.093	6.5	663.2	60.23
SRP	μg L^{-1}	25.0	47.2	0.096	0.0	617.6	35.2
TDN	μg L^{-1}	1,789	1,169	0.000**	606.2	3,544.0	1,495.5
Ammonia	μg L^{-1}	17.1	14.7	0.655	0.0	200.0	15.9
Nitrate	μg L^{-1}	1.9	2.2	0.848	0.0	89.6	2.0
Available N (NO_3+NH_4)	μg L^{-1}	19.0	16.9	0.723	0.2	218.9	17.9
Available N : P ratio		5.1	2.0	0.044**	0.0	83.0	3.6
Magnesium	mg L^{-1}	11.7	6.4	0.000**	0.0	40.0	9.2
Potassium	mg L^{-1}	6.11	2.1	0.000**	0.0	28.3	4.2
Sulfate	mg L^{-1}	18.4	10.5	0.026**	0†	115.1	14.7
Chloride	mg L^{-1}	1.5	1.3	0.708	0.0	16.6	1.4
Conductivity	μS cm^{-1}	240.7	162.5	0.000**	19.3	547.0	206.2
pH		8.4	8.1	0.047**	6.0	10.2	7.6
Turbidity	NTU	3.4	4.1	0.465	0.3	31.0	3.8
DOC	mg L^{-1}	32.5	24.7	0.000**	9.1	61.0	28.8
Water color	mg Pt L^{-1}	100.4	143.4	0.000**	18.2	369.0	120.3
Water depth	m	1.2	1.3	0.128	0.3	1.9	1.3

DOC: dissolved organic carbon, SRP: soluble reactive phosphorus, TDN: total dissolved nitrogen, TDP: total dissolved phosphorus, TP: total phosphorus.
* Significant difference.
† Not detectable.

clearing of the water was observed. These threshold levels for both chlorophyll and SAV resulted in four groups of lakes. These groups are defined as (1) phytoplankton-dominated (with low SAV cover), (2) SAV-dominated (with low phytoplankton), (3) high phytoplankton and SAV (both high values) and (4) low phytoplankton and SAV (both with low values). These four vegetation groups were used in further data analyses. Water chemistry variables were compared among these groups using a Kruskal-Wallis one-way analysis of variance followed by a Kolmogorov-Smirnov two-sample test. These analyses were done using SYSTAT version 10 (SPSS).

Results

Water chemistry variation—The wetland lakes were high in DOC (mean, 28.8 mg L^{-1}), generally dark in color (120.3 mg Pt L^{-1}), and often alkaline or neutral in pH (7.6) (Table 1). Mean depth averaged 1.3 m. In contrast to many boreal shield lakes, most of these lakes had high concentrations of TP and SRP (mean, 123.2 and 35.2 μg L^{-1}, respectively). They also had very low concentrations of available nitrogen (mean 2.0 μg L^{-1} NO_3-N and 15.9 μg L^{-1}NH_4-N), which suggests these shallow lakes may be nitrogen limited (available N : SRP ratio of 3.6 : 1). There was a large range in water chemistry variables; however, the mean concentrations of many of the variables were low, and the distributions were positively skewed (pH and alkalinity). Conductivity averaged 206.2 μS cm^{-1}.

More than 69% of these lakes had naturally high concentrations of TP and could be classified as eutrophic or hypereutrophic. In contrast, <7% of the lakes could be considered oligotrophic. Classification of the lakes on the basis of TP (Table 2) indicated that Chl *a* in the oligotrophic lakes

Table 2. Classification of the 148 lakes on the basis of total phosphorus (TP) concentrations. Phytoplankton (measured as Chl *a*) and submerged aquatic vegetation (SAV) abundance (measured as percentage of cover) in lakes of different trophic status are also given. SAV cover is given as mean rating category (1=0%; 2=<5%; 3=5%–25%; 4=25%–75%; and 5=>75%). See text for further description.

Trophic state	No. of lakes	TP range (μg L^{-1})	Mean TP (μg L^{-1})	Chlorophyll range (μg L^{-1})	Mean chlorophyll (μg L^{-1})	Mean SAV (rating)
Oligotrophic	10	16.0–24.2	20.5	1.4–6.3	3.2	4.0
Mesotrophic	36	31.5–48.2	36.5	1.1–25.2	6.9	3.4
Eutrophic	41	50.9–92.2	72.2	1.6–132.0	21.1	3.2
Hypereutrophic	35	101.9–198.4	143.0	0.9–151.5	41.2	2.9
	26	201.2–726.6	336.6	1.4-343.6	94.4	2.6

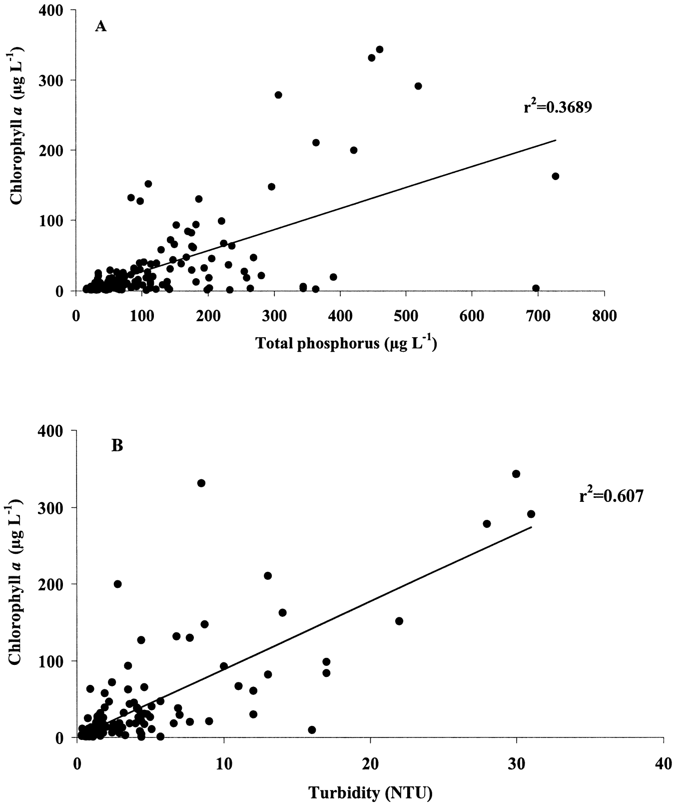

Fig. 2. The relationship between Chl *a* and (A) total phosphorus and (B) turbidity in 148 shallow lakes from northern Alberta.

averaged 3 μg L^{-1}, that in the eutrophic lakes averaged 21 μg L^{-1}, and that in hypereutrophic lakes averaged $>$41 μg L^{-1} (Table 2). The hypereutrophic lakes could be divided into two categories: lakes with TP between 100 and 200 μg L^{-1} and lower in chlorophyll (mean, 41.2 μg L^{-1}), and lakes with TP $>$200 μg L^{-1} and extremely rich in chlorophyll (94 μg L^{-1}).

Relationships between Chl a *and TP*—There was a range in TP concentration of $>$700 μg L^{-1} and a range in Chl *a* concentration of $>$300 μg L^{-1} in the 148 lakes (Table 1). The Chl *a* concentration (a proxy for phytoplankton abundance) was modestly but significantly predicted by TP ($r^2 = 0.37$, $P \leq 0.00$) (Fig. 2A). Clearly, phytoplankton abundance in these shallow lakes was influenced by factors other than phosphorus concentration. Much of the turbidity in the water is associated with phytoplankton populations; Chl *a* concentrations are strongly predicted by turbidity ($r^2 = 0.61$, $P \leq 0.00$; Fig. 2B). Multiple regression analysis indicated that 79.9% of the chlorophyll variance was predictable from NH_4^+, SRP, TP, SO_4^{-2}, Ca^{+2}, HCO_3^-, and pH ($P \leq 0.05$). The other chemical variables in the data set did not have significant predictive contributions.

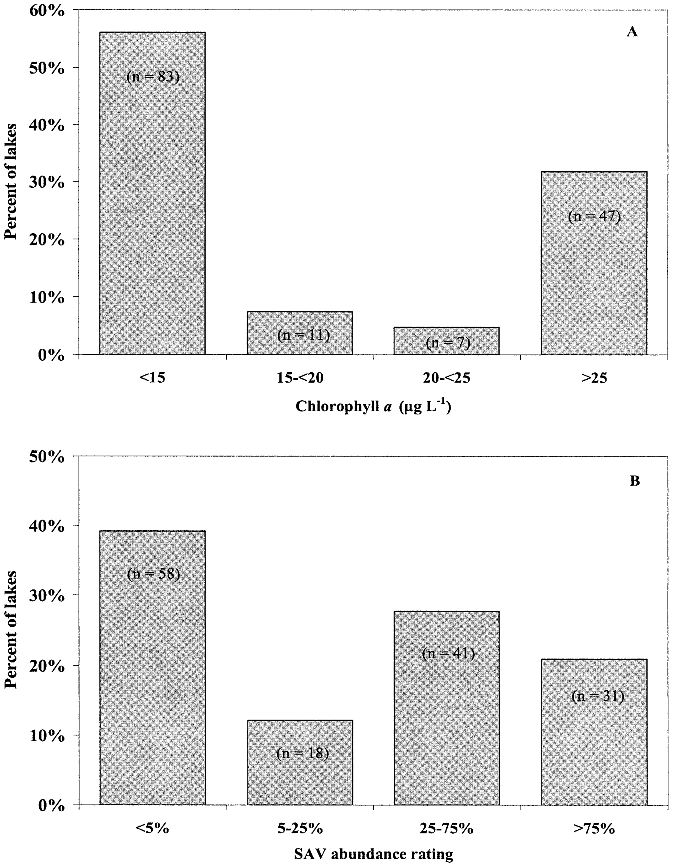

Fig. 3. Frequency distribution of (A) Chl *a* concentration and (B) submersed aquatic vegetation (SAV) cover rating in 148 shallow boreal lakes. The number of lakes for each histogram bar is given in parentheses. There is a bimodal distribution of lakes for both variables, with ~50% of the lakes with abundant/common SAV and 50% with little SAV. Similarly, 56% of lakes have a low abundance of Chl *a*.

Relationship between Chl a *and SAV*—Analysis of the Chl *a* concentrations suggested that there were two main groups of shallow lakes in this part of the western boreal landscape: lakes with lower phytoplankton biomass ($<$15 μg L^{-1}) and lakes with higher phytoplankton biomass ($>$25 μg L^{-1}) (Fig. 3A). There were very few lakes (12%, $n = 18$) with intermediate (15–25 μg L^{-1}) phytoplankton biomass. This bimodal distribution suggests that there are alternate states in terms of Chl *a* (56% of lakes had $<$15 μg L^{-1} Chl *a*, and 32% of lakes had $>$25μg L^{-1}). We used this bimodal pattern to classify the lakes on the basis of lower ($<$20 μg L^{-1}) versus higher ($>$20μg L^{-1}) Chl *a* concentration (*see* Table 3 and ‘‘Materials and methods’’).

SAV cover (estimated by our five cover categories) also showed a bimodal pattern. There were many lakes (39%; $n = 58$) with sparse SAV cover (includes both $<$5% and no SAV) and many lakes (21%, $n = 31$) with abundant SAV cover ($>$75%) (Fig. 3B). To classify the lakes on the basis of SAV abundance, we grouped lakes into those dominated by SAV (25%–75% and $>$75% cover) and those with no, rare, or occasional patches of SAV (0%, $<$5%, and 5%–25%) (Table 3). The 148 lakes were about evenly divided into those with common to abundant SAV and those with occasional to no SAV cover (Fig. 3B).

The distribution of lakes along the gradients of low to high Chl *a* concentration and low to high SAV cover appeared to be bimodal for both parameters, although they

Table 3. Mean water chemistry of lakes in the four groups (defined by thresholds of submerged aquatic vegetation [SAV] and phytoplankton). The number of lakes in each group is given in parentheses. Kruskal-Wallis (K-W) analysis of variance (ANOVA) was used to determine variables that differed among groups (P values from the ANOVA are given). There were two distinct groups of lakes based on total phosphorus (TP) and turbidity but four distinct groups on the basis of chlorophyll and SAV abundance (supporting the arbitrary groupings). Other variables differed among various combinations of lake groups. The significant differences are indicated (A, B, C, and D).

Variable	Units	Phytoplankton dominated (37)	SAV dominated (55)	Phytoplankton and SAV high (17)	Phytoplankton and SAV low (39)	P value from K-W ANOVA
Chl *a*	μg L^{-1}	89.0 A	6.6 B	62.3 A	8.3 B	<0
SAV abundance	Rank category	1.9 A	4.4 B	4.5 B	1.8 A	<0
TP	μg L^{-1}	204.6 A	81.7 B	140.0 A	97.3 B	<0
Turbidity	NTU	8.1 A	1.7 B	5.8 A	1.7 B	<0
TDP	μg L^{-1}	73.8 A	54.7 B	44.6	62.0	0.004
SRP	μg L^{-1}	41.3 A	34.3 B	17.6	38.4	0.005
TDN	μg L^{-1}	1,664.9	1,463.2	1,647.1	1,314.2	NS
Ammonia	μg L^{-1}	16.5	9.4	7.1	28.4	NS
Nitrate	μg L^{-1}	1.2 A	1.7 B	0.7 C	3.8 D	<0
Available N	μg L^{-1}	17.7 A	11.1	7.8	32.2 B	0.035
Available N : P ratio		1.7 A	3.6 B	2.4	5.9	0.018
Magnesium	mg L^{-1}	8.2	11.4 A	8.3 B	7.2 B	0.011
Potassium	mg L^{-1}	3.1	5.6	3.6	3.3	NS
Calcium	mg L^{-1}	28.2	28.6	27.7	25.3	NS
Sulfate	mg L^{-1}	12.7	17.7	14.8	12.3	NS
Chloride	mg L^{-1}	2.0 A	1.2 B	1.9	0.8 B	0.043
Conductivity	μS cm^{-1}	200.2	232.7 A	189.1 B	179.8 B	0.043
pH		7.3	7.8	7.8	7.3	NS
DOC	mg L^{-1}	30.4	27.3	30.9	28.6	NS
Water color	mg Pt L^{-1}	122.2	101.1 A	122.7	144.5 B	0.048
Water depth	m	1.3	1.2	1.1	1.4	NS

DOC: dissolved organic carbon, NS: not significant, SRP: soluble reactive phosphorus, TDN: total dissolved nitrogen, TDP: total dissolved phosphorus.

were not necessarily concordant. In general, the lakes with lower Chl *a* concentrations had higher amounts of SAV, whereas lakes with higher concentrations of Chl *a* had lower amounts of SAV. However, there were also some lakes with both high Chl *a* and SAV, and there were lakes with both low Chl *a* and low SAV (see Table 3). Even with this generally inverse relationship between Chl *a* and SAV cover, the regression between them was poor ($r^2 = 0.03$), perhaps because SAV cover is rated with five categories and not on a continuous scale (results not shown).

Ordination of shallow lakes—PCA was used to examine multivariate relationships among lakes. The ordination using water chemistry variables revealed no clear difference between the data sets from the two areas (Utikuma and Mistehae; data not shown). Individual lakes are separated along axis 1 by a gradient of TP concentration and along axis 2 by inverse gradients of NO_3^- and conductivity, Mg^{+2}, and Cl^- concentrations (Fig. 4A). Phosphorus (TP, TDP, and SRP) explains 61.3% of the variance in site scores on axis 1, whereas available nitrogen, NO_3^-, and turbidity explain 34.1% of the variance on axis 2. The four lake groups (arbitrarily defined by chlorophyll and SAV in Table 3) have been plotted on the PCA. In the final PCA (Fig. 4A), the phytoplankton-dominated lakes (closed circles) were positioned primarily in the lower right quadrant, whereas the SAV-dominated lakes (shaded squares) were positioned mainly on the left side of axis 1. Most of the phytoplankton-dominated lakes are at the low end of the NO_3^- gradient and the high end of the conductivity, Mg^{+2}, and Cl^- gradient. Results from the indirect ordination analysis were not exactly the same as the arbitrary lake classification (based on thresholds), because PCA organizes the lakes along gradients in relation to the actual value for a particular variable. Lakes organized along the chlorophyll trajectory were based in part on the actual chlorophyll concentration in the lake. Because the chlorophyll values formed a gradient and not discrete groups, the ordination scores are also a gradient of values. For example, lakes with chlorophyll values of 19 and 21 were placed close together on the trajectory, even though the lakes would be placed within different groups when our threshold of 20 μg L^{-1} was used. Ordination scores would be close for those lakes, but the symbols would be different.

To examine the SAV-dominated lakes in more detail, we removed the other lake categories (plankton-dominated and plankton with SAV) from the PCA biplot and labeled the SAV lakes by lake trophic status. The lakes with high SAV cover were distributed across the TP concentration gradient from oligotrophic to hypereutrophic status (Fig. 4B). However, most of the SAV-dominated lakes were positioned at the lower end of the TP concentration gradient on PCA axis 1.

PCA of the 148 lakes, using the environmental data as pseudo species, suggested that TP, TDP, SRP, color, conductivity, Cl^-, Mg^{+2}, NO_3^-, available N, and the N : P ratio are important variables that influence (or are influenced by) SAV

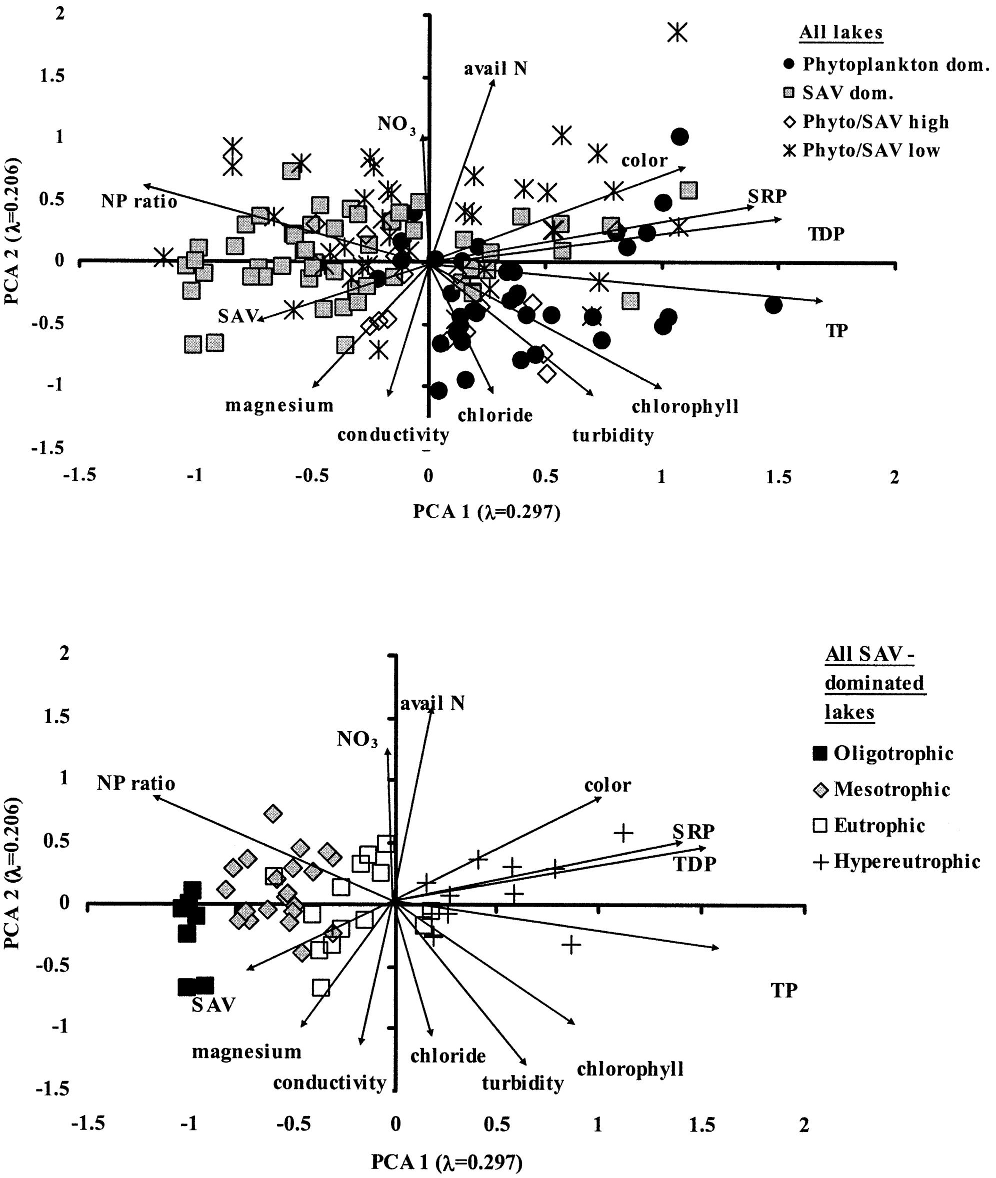

Fig. 4. (A) Principal components analysis (PCA) of 148 lakes with 13 variables used as pseudo species. (A) Symbols correspond to the lake groups defined in Table 3. (B) PCA of submersed aquatic vegetation (SAV)–dominated lakes only ($n = 55$). (B) Symbols correspond to the trophic status of the lakes based on TP concentrations. Most of the lakes dominated by SAV are found at the left of axis 1 (primarily TP gradient), but some lakes with high SAV also have high TP concentrations.

and phytoplankton. Mean concentrations of these variables differed between at least two groups of lakes (Table 3). TWINSPAN analysis of the 148 lakes showed a similar pattern of grouping lakes by TP concentration, Chl *a* concentration, and SAV abundance (results not shown).

Water quality of SAV-dominated lakes versus phytoplankton-dominated lakes—On the basis of the bimodal distribution of Chl *a* and SAV (Fig. 3A,B) and the results of the indirect ordination (Fig. 4A), we classified the lakes into four main categories of aquatic productivity. This resulted in the creation of four lake groups (Table 3) with differing vegetation type and cover.

The water quality of the shallow lakes differed among the four vegetation classes in a number of variables (Table 3). Although there are obviously significant differences in SAV and Chl *a* (because that was how the classes were defined), there were also significant differences in TP, SRP, NO_3^-, available nitrogen ($NH_4^+ + NO_3^-$), the ratio of available N : P, Mg^{+2}, conductivity, turbidity, and water color. The clearest lakes were those dominated by SAV. Despite the fact that many of these lakes were embedded in bog or fen complexes, they were neutral to alkaline in pH and had high phosphorus concentrations.

Lakes dominated by phytoplankton were generally hypereutrophic (mean TP, $>200\ \mu g\ L^{-1}$), whereas lakes dominated by SAV (and lower Chl *a*) had lower TP ($82\ \mu g\ L^{-1}$). Lakes dominated by SAV also had higher concentrations of Mg^{+2}

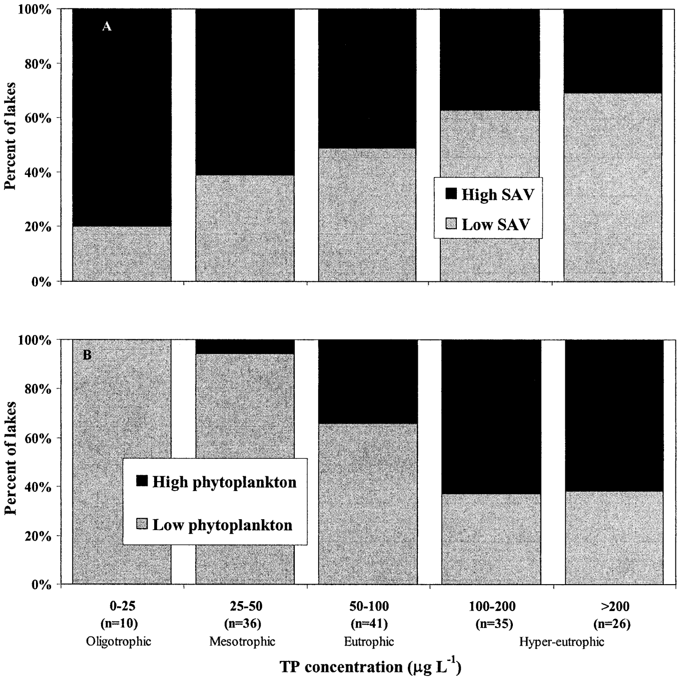

Fig. 5. Trophic status of 148 wetland lakes based on (A) submersed aquatic vegetation (SAV) cover and (B) phytoplankton abundance (Chl *a* concentration). Across this gradient from low to high total phosphorus concentration, there is a decreasing number of lakes with high SAV and a concomitant increase in frequency of lakes with high phytoplankton. In the mid–phosphorus concentration range (25–100 μg L^{-1}), most of the lakes have low chlorophyll concentrations, whereas SAV cover is highly variable.

and conductivity and were clearer (lower water color and lower turbidity) than lakes with high Chl *a* concentrations (phytoplankton-dominated and high phytoplankton/SAV lakes) (Table 3).

Nitrate concentrations in lakes were low regardless of vegetation class (Table 3). Three of the vegetation classes had mean ratios of available N : P <4 : 1, which suggests that nitrogen was likely limiting to phytoplankton growth. Of interest, there were no significant differences in NH_4^+ or TDN concentrations, although available N ($NH_4^+ + NO_3^-$) was lower in lakes with high SAV (Table 3); conversely, available N was higher in the phytoplankton-dominated lakes than in SAV-dominated lakes.

Existence of alternative vegetative states—To determine whether the bimodal frequency distribution of Chl *a* and SAV (Fig. 3A,B) existed across the TP gradient, we examined the relationship among TP concentration, SAV cover, and Chl *a* concentrations in more detail. Lakes were separated by the trophic categories used in Table 2. The frequency of lakes with high versus low SAV cover (Fig. 5A) and then, independently, high versus low chlorophyll concentration (Fig. 5B) were determined for each of the trophic categories from Table 2. For each of the five TP concentration categories, the percentage of lakes falling into each of the SAV cover categories (Fig. 5A) and Chl *a* categories (Fig. 5B) were calculated.

At low TP levels (0–25 μg L^{-1}), 80% of lakes had high SAV, whereas, at the highest TP levels (>200 μg L^{-1}), only 35% of lakes had high SAV (Fig. 5A). As TP concentration increased, the percentage of lakes with high Chl *a* concentrations increased (Fig. 5B). At lower TP values (0–25 μg L^{-1}), all the lakes had low phytoplankton concentrations (<20 μg L^{-1}), whereas, at TP >200 μg L^{-1}, >65% of lakes had high phytoplankton concentrations. At the intermediate TP values, either phytoplankton or SAV can dominate lakes, as suggested by the alternative-state hypothesis. However, the high-phosphorus lakes (>200 μg L^{-1}) can also have alternate states (35% of lakes have lower chlorophyll values and higher SAV cover).

Discussion

Nutrients in shallow western boreal lakes—The lakes in our study area are similar in nutrient status to larger boreal lakes in Alberta, with almost 70% of our lakes falling into eutrophic or hypereutrophic categories (Table 2). There are many lakes in western Canada that are situated on thick glacial till rich in nutrients; these lakes are often eutrophic (Prepas et al. 2001). In contrast, boreal lakes on shield bedrock in both eastern and western Canada are typically oligotrophic (Schindler 1978; Moser et al. 1998). In areas unaffected by human activities, watershed geology is the most important factor that determines phosphorus concentrations in western boreal lakes (Moser et al. 1998). Despite the geological conditions, the lakes in our study area are less eutrophic than lakes in England (Moss et al. 1998), Denmark (Jeppesen et al. 2000), or parts of Florida (Brown et al. 2000), where lakeshores and watersheds are heavily developed.

Alternative stable states in shallow boreal lakes—The lakes included in the present study have a bimodal frequency distribution across the gradients of chlorophyll concentration and SAV cover (Fig. 3A,B). In contrast to the bimodal distribution of SAV and chlorophyll, TP concentrations are not bimodally distributed; there is an increasing frequency of lakes along the phosphorus concentration gradient (Table 2). This results in a poor linear relationship between TP and chlorophyll concentration (Fig. 2A) and between TP and SAV abundance (data not shown).

Nearly 50% of the shallow lakes had dense populations of SAV (common or abundant on the rating scale) (Fig. 3B). Given the generally shallow depth (mean depth, 1.3 m), it is surprising that more lakes are not dominated by SAV. Presumably, the high phosphorus concentrations, flocculent bottom, stained color, and deep winter ice (the lakes may freeze to the bottom, pulling the SAV out) may reduce SAV populations and permit phytoplankton to dominate in these shallow lakes.

The number of lakes with high SAV cover gradually decreased across the TP gradient (Fig. 5A), whereas the number of lakes with high phytoplankton (>20 μg Chl *a* L^{-1}) concentrations increased sharply above 50 μg TP L^{-1} (Fig. 5B). The bimodal distribution of chlorophyll and SAV abundance suggests that lakes tend to exist in alternative states dominated by one vegetative form or the other (Fig. 3A,B).

There is also evidence to show that these alternative states occur across a nutrient gradient. At lower nutrient levels (<50 μg TP L^{-1}), most of the lakes had abundant SAV, whereas, at high nutrient levels (>100 μg TP L^{-1}), most of the lakes had high chlorophyll concentrations (Fig. 5B). However, even some of the hypereutrophic lakes had a dominant or codominant SAV community. Lakes with intermediate nutrient levels (50–100 μg TP L^{-1}) appeared to also have codominance or dominance by SAV. Thus, although the TP concentration is important, it does not completely explain the alternative dominant states of primary production. Nitrogen concentrations, lake depth, lake size, and other factors can also influence the SAV state (Scheffer 1997).

Potential control of the alternative states in shallow boreal wetland lakes—The SAV-dominated, or clear-water, state can exist over a wide range of nutrient concentrations but has been found most often between 50 and 150 μg L^{-1} TP (Scheffer et al. 1993; Moss et al. 1994). Above this threshold of TP, lakes may switch to the more turbid phytoplankton state. This suggests that our lakes in the intermediate nutrient ranges could potentially flip to the alternative stable state if nutrient loading rates are altered through watershed disturbance.

Differences in depth, lake size, and other factors (N concentrations) may affect the switch from one vegetative state to another. We found ~35% of the eutrophic and hypereutrophic lakes to have a high abundance of SAV (Fig. 5A). This may be due to the extremely shallow depth of these lakes and the moderating influence that macrophytes have on maintaining their preferred clear-water environment. Inside a macrophyte bed, plants (Blindow 1992; Weisner et al. 1994) and epiphytic algae reduce the nutrient concentrations available to phytoplankton, and the plants reduce sediment resuspension, provide a refuge for zooplankton grazers, and may release allelopathic chemicals (Scheffer et al. 1993; van Donk and van de Bund 2002). The absence of fish has been shown to have a significant effect on the water clarity in shallow lakes, as evidenced by the change in zooplankton composition after a fish kill (e.g., Hanson and Butler 1994). On the basis of a more detailed study currently in progress in the Utikuma area, it is likely that the lakes dominated by phytoplankton are slightly deeper (S.E.B., unpubl. data). Water levels may be the critical factor causing the switch between SAV and phytoplankton in these generally eutrophic, fishless lakes. Changes in water levels (in combination with low temperatures) have been responsible for long-term switches from one alternative state to another in other areas (Mitchell 1989; Blindow et al. 1993; Scheffer et al. 1993). Recent climate trends with long periods of drought may be making North American boreal lakes even shallower and contributing to SAV dominance. However, other hydrological and physical factors, including long water residence time and infrequent mixing, positively influence high concentrations of cyanobacteria (Elser 1999).

Nitrogen also may play a role in controlling vegetation. Scheffer and Jeppesen (1998) suggested that the clear-water state was unlikely to occur above 50–150 μg L^{-1} TP unless the N input is low. Most of the lakes can be considered limiting in N relative to P for growth of plants and algae (available N : P ratios $<6:1$). In fact, N availability is limited in lakes of all vegetation classes (Table 3) (sensu Redfield). Mean nitrate concentrations differed in lakes with different vegetation classes (Table 3). Nitrate concentrations were highest in the lakes with low primary production (both phytoplankton and SAV) and lowest in lakes with high primary production (both phytoplankton and SAV). Stepwise multiple linear regressions indicated that TP, along with NH_4^+, SRP, SO_4^{-2}, Ca^{+2}, HCO_3^-, and pH, significantly influence the concentration of chlorophyll in our shallow lakes. Nitrate, available N, and magnesium were important variables separating the lakes along the second PCA axis (Fig. 4A).

Although nutrients or water depth may control phytoplankton versus SAV abundance, the system may also be influenced or regulated from the top down by grazing. There are numerous references on the role of planktivorous fish and zooplankton grazers on phytoplankton in deep (Carpenter and Kitchell 1993) and shallow lakes (Jeppesen et al. 1998). Large-sized zooplankton (*Daphnia*) can change the community structure of phytoplankton in shallow lakes, leading to larger sized phytoplankton and reduced shading by phytoplankton and thereby allowing an increase in SAV (Jeppesen et al. 2000). Planktivorous fish typically feed so extensively on large-sized zooplankton that the algal community shifts to small-celled species that shade out SAV (Mitchell 1989). Removal of planktivorous fish can have ‘‘cascading effects,’’ which are observed as improved macrophyte cover and water clarity (Hanson and Butler 1994). One unique aspect of our lakes is that many have no fish (Conlon 2002). In a survey of 24 shallow lakes that we examined in detail, only four had fish (S.E.B., unpubl. data). Most fish die because the lakes freeze to the bottom in winter. Under some conditions, fish can migrate from the deeper lakes (>2 m), but the correct hydrological conditions must prevail. Lakes may switch in dominance from SAV to phytoplankton because fish are reintroduced at periodic intervals. Periodic droughts and lowering of water tables may foster shallow water (favoring SAV) and winter-kill of fish (also favoring SAV). However, many of these shallow lakes are isolated from surface flows and receive much of their water from ground water, so fish may not be able to reinvade to play a major role in regulating trophic dynamics. Large macroinvertebrates are abundant in these shallow lakes and are generally more abundant in lakes without fish as opposed to lakes with fish (Mallory et al. 1994). This presents a trophic structure that is different than the one found in deeper lakes, where there are planktivorous and sometimes piscivorous fish present. There has been relatively little study of the ability of macroinvertebrates to control the trophic cascade, except for some studies conducted in alpine fishless (Paul et al. 1995) or deep lakes (Wahlström and Westman 1999).

The relative role of nutrient input (bottom-up) versus grazing (top-down) control on the alternative states has not been well studied in shallow wetland lakes. In fact, wetland lakes may be unique, in that physical processes (lowered water levels) and winter fish kills may be more important than in the deeper ‘‘shallow lakes’’ (2–5 m). Although >60% of our shallow lakes are clearly in one alternative state or the other, we do not know whether or how frequently they switch.

There are very little data available on these processes in shallow lakes that are relatively unaffected by human activity; previous studies on shallow eutrophic lakes with alternative states focused on lakes that have been anthropogenically modified (e.g., Brown et al. 2000; Jeppesen et al. 2000). The literature generally suggests that a reduction in nutrient concentrations alone does not necessarily reduce the abundance of phytoplankton and promote growth of SAV; instead, nutrient reduction combined with biomanipulation (e.g., fish removal and grazer populations) are needed to cause a switch in a lake from the turbid to the clear-water state (e.g., Hanson and Butler 1994; Jeppesen et al. 1997; Moss et al. 1998). Studies have suggested that macrophytes will become established within a few months if there is sufficient available light, even for a short time, and if propagules are readily available (Perrow et al. 1997). The boreal lakes examined here offer a unique opportunity to study the processes controlling the alternative states in lakes with limited direct anthropogenic impacts and without fish.

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