

Spatial heterogeneity in trophic status of shallow lakes on the Boreal Plain: Influence of hydrologic setting

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[1] We used metrics of surface water and groundwater connectivity as explanatory variables in nonparametric regression models to explain the spatial heterogeneity in trophic status of shallow lakes. The concentration of chlorophyll *a* (Chl *a*) was used as an indicator of trophic status and was estimated from 17 Landsat images acquired during the end of summer (August) over a 20-year period from 1984 to 2003. A long-term median of Chl *a* was computed for each of 40 lakes on the basis of the 17-year data set. Hydrologic metrics explained 72% of the spatial variation in Chl *a*. The regression tree showed that lakes with a higher concentration of calcium plus magnesium (Ca + Mg) exhibited higher Chl *a* than lakes with a lower Ca + Mg. We hypothesized that this trend was a result of either higher internal nutrient loading in high Ca + Mg lakes due to groundwater discharge or differences in surficial geology. Among high Ca + Mg lakes, lakes with no inflowing streams had lower Chl *a*, while connected lakes had higher Chl *a*, possibly reflecting enhanced nutrient delivery to lakes connected to the stream network. Among low Ca + Mg lakes, lakes with larger wetland cover in their drainage basins had lower Chl *a*, while lakes with smaller wetland cover in their drainage basins had higher Chl *a*, possibly reflecting differential water loading rates between small and large wetlands that lead to either Chl *a* concentration or dilution. These results suggest that relatively simple hydrologic metrics can be used to predict the trophic status of lakes in this area of the boreal forest.

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1. Introduction

[2] Boreal aquatic ecosystems, such as shallow lakes, are at increasing risk to anthropogenic impacts on their hydrology, biogeochemistry and ecology [Schindler, 1998]. The Boreal Plain of northern Alberta especially, has a large presence by forestry, oil and gas and agriculture industries, each with different degrees of impacts on aquatic ecosystems [Alberta Environmental Protection, 1998]. Scientifically informed management is needed in order to alleviate and mitigate these impacts [Szaro and Peterson, 2004]. The best management strategies are based on a sound understanding of the dominant processes that control the flow of matter and energy in boreal landscapes in undisturbed settings [Buttle *et al.*, 2000, 2005]. Monitoring of the spatial and temporal changes in key ecosystem properties allows us to understand basic ecosystem functioning as well as to provide a baseline to which future system states can be compared.

[3] Trophic status of lakes is an important ecosystem property to monitor because it integrates hydroecological

processes occurring within the drainage basin and the lake itself. Trophic status refers to the potential of an aquatic system to support biological production at a variety of trophic levels. Trophic status can be estimated using physical, chemical and biological approaches [Carlson, 1977]. Trophic status is often estimated by measuring the concentration of chlorophyll *a* (Chl *a*) in water [cf. Thiemann and Kaufmann, 2000], which is a good proxy for algal biomass, one of the main components of primary production.

[4] Trophic status can be monitored at multiple spatial and temporal scales. At local spatial scales (i.e., variation within a lake) indicators of trophic status are likely to reflect spatial heterogeneities in trophic interactions, including predation and competition [Wiley *et al.*, 1997]. Understanding the nature of mechanisms controlling variation at local spatial scales requires site-specific sampling of the physical, chemical and biological components of each lake. At regional scales (i.e., variation between many lakes) indicators of trophic status are likely to reflect spatial heterogeneities in landscape factors, such as geology, soils, and climate, that determine water and nutrient mobilization from drainage basin to lake [Wiley *et al.*, 1997; Devito *et al.*, 2000, 2005a]. Understanding the nature of mechanisms controlling variation at regional scales requires the characterization of the physical setting of each lake. Recent advances in remote sensing, digital terrain analysis, and geographic information systems have given rise to studies of hydroecological patterns and processes at these broader spatial scales [Pietroniro and Leconte, 2005]. Monitoring

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ecosystems at larger spatial and temporal scales allows for the detection of patterns that would be invisible at shorter scales [Magnuson, 1990; Swanson and Sparks, 1990].

[5] Sass *et al.* [2007] analyzed the natural variation in summer trophic status of shallow lakes (lake area >5 ha, mean depth <3.2 m) located on the Boreal Plain over a 20-year period and found that of the total variation in Chl *a*, approximately 50% was attributed to the space factor, 10% to the time factor, and 40% to the space × time factor (which also included the error term). Synthesizing conceptual models from Wiley *et al.* [1997], Blenckner [2005], and Devito *et al.* [2005a], Sass *et al.* [2007] hypothesized that the sources of spatial and temporal variation in trophic status were driven by climatic and hydrologic properties of the landscape. The role of climate in regulating temporal variability was explored in a companion paper [Sass *et al.*, 2008]. The focus of this paper was to elucidate the source of spatial heterogeneity in trophic status in the data set derived by Sass *et al.* [2007].

[6] Previous research has indicated that hydrologic properties of the landscape may play a key role in determining why lakes in the same region have different trophic status [Devito *et al.*, 2000]. These studies have shown that hydrological dynamics control the transfer of the limiting nutrients into the water column of lakes. The limiting nutrient on algal production in this region is phosphorus (P) with total nitrogen to total phosphorus ratios in excess of 20 [Prepas and Trew, 1983; Prepas *et al.*, 2001; Bayley *et al.*, 2007]. Hydrologic control on P transport has been demonstrated in process-based studies as either surface and shallow groundwater transfer of P [Evans *et al.*, 2000; Ferone, 2001; Macrae *et al.*, 2005], hydraulic forcing of P from lake bottom sediments [Shaw *et al.*, 1990] or stream transport of P [Cooke and Prepas, 1998]. At the regional scale, Sass *et al.* [2008] found evidence for climatic control on Chl *a* and by inference on P, where 64% of the interannual variation in Chl *a* was explained by growing season effective precipitation. These results suggested that the influence of hydrology seems to be very important in this subhumid landscape.

[7] In this study, we tested the hypothesis that surface and groundwater hydrologic connections between lakes and their drainage basins play an important role in controlling the spatial differences in trophic status. We use the term surface water to refer to both saturated overland flow generated in wetlands and streamflow. We hypothesized that surface water and groundwater connectivity between lakes and their drainage basins are important landscape properties regulating phosphorus movement and consequently the trophic status of lakes. Whereas Sass *et al.* [2008] focused on the role of water in influencing the temporal variability in trophic status, in this paper we focused on the pathways of water through catchments and explored hydrologic influences on the spatial heterogeneity in trophic status of lakes situated within a regional drainage basin on the Boreal Plain.

[8] We postulated a priori the mechanisms through which hydrologic connectivity might be controlling the trophic status of lakes (Table 1). We expected that saturated overland flow would be especially important in controlling phosphorus movement as most of the biogeochemically available phosphorus is stored in the top layer of soil

[Macrae *et al.*, 2005]. Previous research on the Boreal Plain has indicated that as the topsoil layers saturate because of a rising water table, the phosphorus stored in these soil layers (e.g., leaf-humic-fibric layer) has the potential to be flushed to receiving surface waters [Evans *et al.*, 2000; Macrae *et al.*, 2005]. Therefore, we expected that lakes well connected to contributing areas of phosphorus (i.e., ephemeral draws and wetlands) would exhibit higher Chl *a*. Similarly, we expected lakes that were receiving water from upstream lakes to show higher Chl *a* because of increased nutrient input [Cooke and Prepas, 1998].

[9] We also expected groundwater connectivity through subsurface flow paths to play a role in influencing phosphorus transfer to lakes by controlling surface and near-surface water dynamics [Devito *et al.*, 2000]. Studies have shown that the concentration of calcium plus magnesium Ca + Mg (mg L⁻¹) in lakes was useful in defining the interactions of a lake with the groundwater flow system in northern Wisconsin [Kratz *et al.*, 1997; Webster *et al.*, 1996, 2000] and this approach has been applied on the Boreal Plain where surficial geology is much more complex [Devito *et al.*, 2000]. Ca + Mg, and similar solutes, increase in concentration as the groundwater flow path length increases because of increased time to interact with the soil matrix. Therefore, Ca + Mg in groundwater has been used to infer the source of water. For example, lakes that have large concentrations of solutes are thought to receive groundwater from longer, regional flow paths [Webster *et al.*, 1996; Devito *et al.*, 2000]. On the Boreal Plain, high Ca + Mg in groundwater was associated with lower total dissolved phosphorus concentrations [Evans *et al.*, 2000; Ferone, 2001; Gibbons, 2005]. We expected that lakes receiving water from longer flow systems would have lower phosphorus loading because of adsorption of phosphorus to soil particles [Ferone, 2001; Macrae *et al.*, 2005] and consequently lower Chl *a* than lakes receiving water from shorter-flow systems which would have higher concentrations of phosphorus originating from near surface organic materials.

[10] To test these hypotheses, we completed the following steps: (1) estimated surface water and groundwater connectivity to each lake; (2) estimated long-term median in summer Chl *a* for each lake; and (3) related metrics of surface water and groundwater connectivity to the spatial variation in Chl *a*. Our study was based on 40 lakes for which we were able to estimate the long-term median (based on 17 years of data) in summer Chl *a* from 1984 to 2003 and the corresponding hydrologic metrics. We used a combination of satellite remote sensing, digital terrain analysis, and ground-based measurements to derive the metrics of hydrologic connectivity for our study lakes.

2. Study Area

[11] The study area comprises the upper part of the Utikuma River drainage basin, which is located on the Boreal Plain ecozone in north-central Alberta (Figure 1). The Utikuma River drainage basin is characterized by flat to gently undulating glaciated terrain with depositional landforms (i.e., moraines) interspersed by glaciofluvial landforms (i.e., outwash plains) and glaciolacustrine landforms (i.e., clay plains) overlying marine shales of the Upper Cretaceous Smoky Group [Hamilton *et al.*, 1999] (Figures 2a and 2b). The depth of the glacial sediments

Table 1. Description of Landscape Controls Considered to Be Important in Controlling the Spatial Heterogeneity in Lake Trophic Status^a

Landscape Control	Hypothesized Hydrologic Mechanism	Trophic Status Prediction	Metric ^b	Measurement	Result	Interpretation
Surface water connectivity: saturated overland flow ^c	Surface water contributions increase as wetland cover increases; higher wetland cover results in higher P loading because of large source area and mobility of P under reducing conditions	Higher percentage of wetlands in contributing area = higher Chl <i>a</i>	Percent wetland	Radar remote sensing of wetlands	Higher percentage of wetlands in contributing area = lower Chl <i>a</i>	Higher wetland cover results in higher runoff ratio and P dilution
Surface water connectivity: streamflow ^d	Surface water contributions increase as stream inputs increase; more stream inputs result in higher P imports; but modified by P exports	More upstream lakes = higher Chl <i>a</i>	Lake connectivity and lake ordering	Digital terrain analysis to estimate stream connections between lakes	More upstream lakes = higher Chl <i>a</i>	P delivery from upstream lakes
Groundwater flow path length ^e	P is reduced in longer flow paths because of adsorption	Higher Ca + Mg (longer flow paths) = less Chl <i>a</i>	Ca + Mg	Water sample from lake	Higher Ca + Mg = higher Chl <i>a</i>	More P in lakes with higher Ca + Mg because of P release from lake sediments due to longer flow paths or more P in lakes with higher Ca + Mg because of richer surficial geologic unit in both P and Ca + Mg

^aP, concentration of phosphorus; Chl *a*, concentration of chlorophyll *a*; Ca + Mg, concentration of calcium plus magnesium.

^bFor derivation of metrics refer to sections 3.1 and 3.2 of text.

^cBased on concepts presented by *Devito et al.* [2000].

^dBased on concepts presented by *Devito et al.* [2000], *Riera et al.* [2000], and *Martin and Soranno* [2006].

^eBased on concepts presented by *Devito et al.* [2000] and *Webster et al.* [2000].

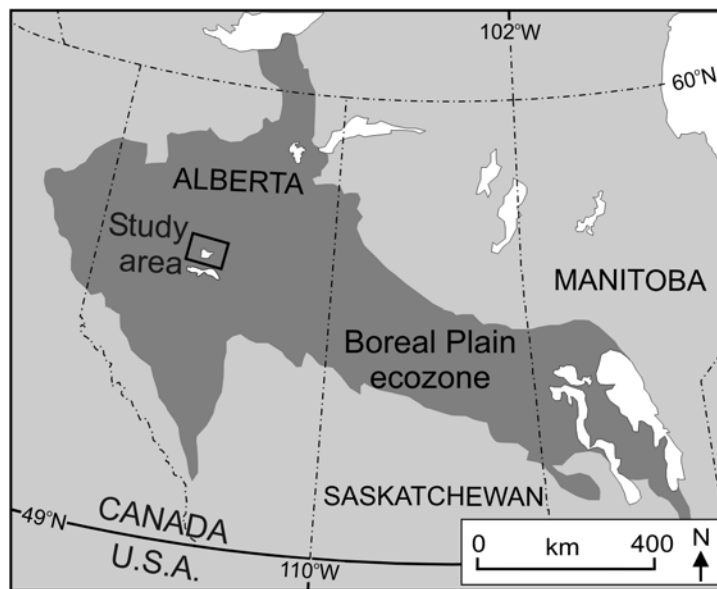


Figure 1. Location of study area. Ecozone boundary based on *Ecological Stratification Working Group* [1995].

ranges from 40 to 240 m [Pawlowicz and Fenton, 2005], making these surficial deposits critical in controlling surface water and groundwater dynamics. In terms of composition, morainal deposits comprise areas of finer sediments such as clay and silt; glaciofluvial deposits comprise areas of coarser sediments such as sand; and glaciolacustrine deposits comprise areas of fine sediments such as clay [Paulen *et al.*, 2004]. All three surficial deposits may be covered by peatlands or areas where at least 0.4 m of organic matter has accumulated. Soils on the better drained till and outwash deposits are dominated by Orthic and Podzolic Gray Luvisols [Wynnyk *et al.*, 1963]. All upland soils are covered by a leaf-humic-fibric (LFH) layer, which ranges in depth from 0.02 to 0.1 m [Wynnyk *et al.*, 1963]. Vegetation is dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch) in low-lying areas and by trembling aspen (*Populus tremuloides* Michx.) in upland areas (Figure 2c).

[12] Low topographic relief in the Utikuma River drainage basin, where the maximum height difference between regional topographic low and high is not more than 200 m, creates the potential for longer, more regional groundwater flow systems [Tóth, 1963] (Figure 2d). Although, precipitation and evapotranspiration dominate the water balance, there is large variability in the type of interaction of groundwater with aquatic systems [Ferone and Devito, 2004; Smerdon *et al.*, 2005]. Similarly, surface runoff is small compared to precipitation and evapotranspiration but becomes important when soil storage has been exceeded [Devito *et al.*, 2005b]. In a subhumid climate where potential evaporation equals or slightly exceeds precipitation inputs, external sources of water may be required in the long-term maintenance of wetlands [Price *et al.*, 2005]. Although representing relatively small percentages of the annual water balance, surface runoff and groundwater flows can potentially supply water to hundreds of shallow lakes and wetlands of this region [Devito *et al.*, 2005a].

[13] The shallow lakes (<3.2 m) range in size from 0.01 ha to 3000 ha (median = 3 ha). Lakes are naturally nutrient rich with high concentrations of phosphorus ($12.4\text{--}670.4\ \mu\text{g TP L}^{-1}$), nitrogen ($618\text{--}5230\ \mu\text{g TN L}^{-1}$) and dissolved organic carbon ($16.8\text{--}705.1\ \text{mg DOC L}^{-1}$) [Bayley *et al.*, 2007]. Primary production takes the form of algal production and/or submersed aquatic vegetation (SAV) production. For more information on biological production in these shallow lake ecosystems refer to Sass *et al.* [2008], Bayley and Prather [2003], and Bayley *et al.* [2007].

3. Methods

[14] The selection of the study lakes was driven by multiple considerations as part of a multiyear monitoring program for the Hydrology, Ecology and Disturbance (HEAD) of western boreal lakes project. As spatial differences in climate were assumed to be negligible, the most important consideration in lake selection was that each of the three main glacial landforms (i.e., clay plain, outwash plain, and moraine) was well represented in order to capture the heterogeneous surficial deposits with the potential for a continuum of hydrologic responses. Further limitations on lake selection were imposed by satellite remote sensing of trophic status of lakes (see below). A total of 40 lakes were identified as suitable for our study objectives. The study lakes ranged in size from 7 ha to 450 ha with a median size of 42 ha. These 40 lakes are a subset of the 76 lakes analyzed by Sass *et al.* [2007, 2008].

3.1. Surface Water and Groundwater Connectivity

[15] Indicators of surface water connections were based on land-to-lake connectivity (i.e., saturated overland flow through wetlands) and lake-to-lake connectivity (i.e., streamflow) (Table 1).

[16] Surface water connections to lakes through wetlands were mapped in a study by Sass and Creed [2008]. First, a simple three category (nonsaturated, saturated, or inundated) classification system was developed on the basis of in situ

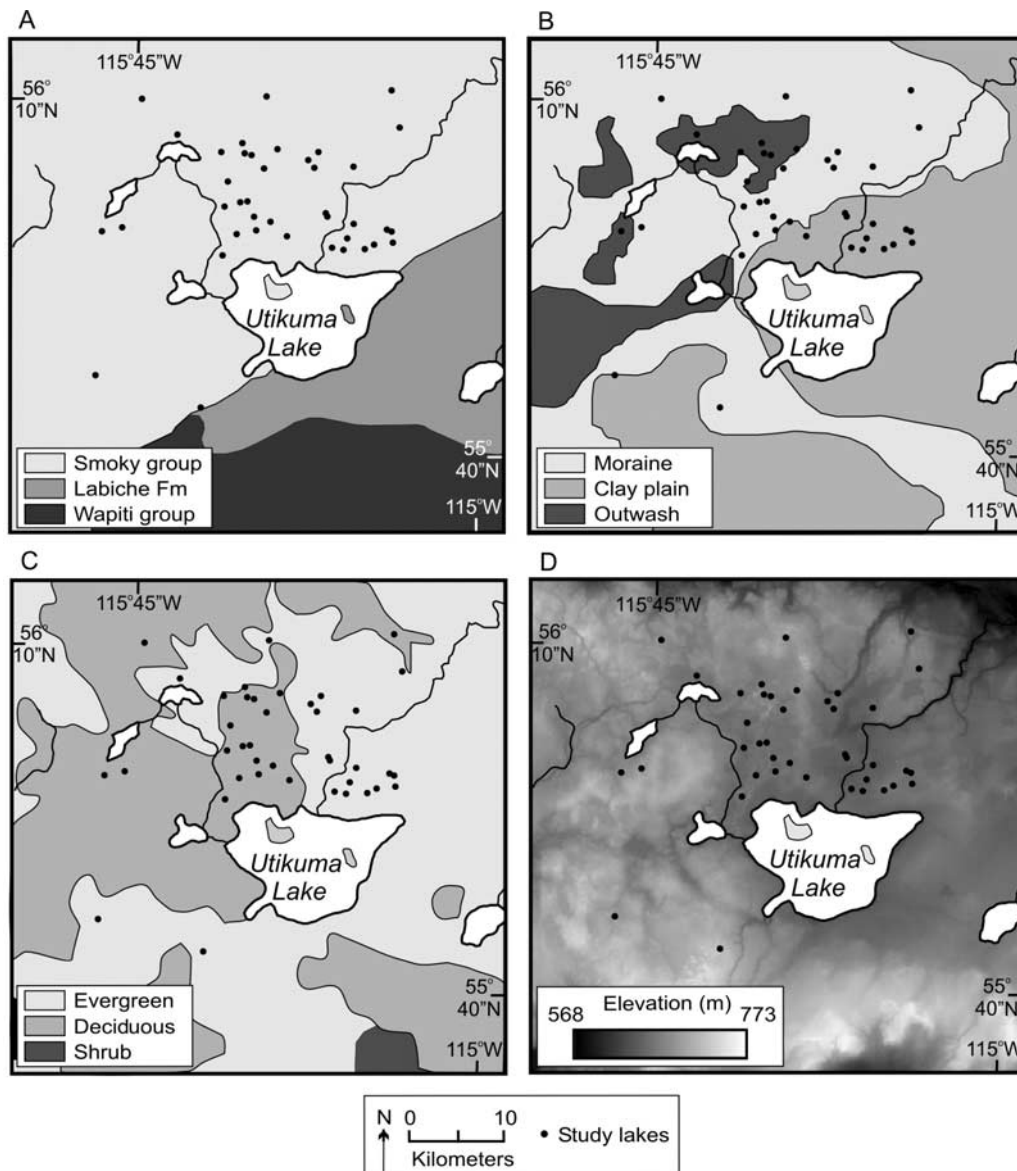


Figure 2. Maps of (a) bedrock geology, (b) surficial geology, (c) vegetation, and (d) topography of the study area overlaid with the locations of the forty study lakes.

soil moisture data, collected during four dates in 2004 with coincident satellite and in situ data. The satellite imagery was acquired by the European Remote Sensing (ERS) satellite, which is an active microwave sensor operating at C band (0.053 m wavelength) [Attema, 1991] and has been used for hydrologic mapping at regional scales [Moran *et al.*, 2004]. The hydrologic classification scheme was then applied to nine archived ERS images captured between 1992 and 2004 during the month of August. Wetlands were defined by collapsing the saturated and inundated classes. These spatial layers were used in the current study to calculate the long-term average of percent wetland within the contributing area (%Wet) and total wetland area within the contributing area normalized by lake area (Wet/Lke). Furthermore, variables were computed by only considering the portion of the wetlands within the contributing areas that were connected to the lake (%Wet_{CON}, Wet/Lke_{CON}). The contributing areas to lakes were defined in two different

ways: (1) the topographically derived drainage basin (total catchment area minus lake area); and (2) the area within a 100 m buffer around each lake, reflecting riparian influences only [Martin and Soranno, 2006]. This constant width buffer approach to defining the contributing area was used to deal with the possibility that the effective contributing area of each lake was much smaller than the topographic watershed [Devito *et al.*, 2005a]. Identifying reasonable hydrologic response units on the Boreal Plain is an active area of research [Devito *et al.*, 2005a]. Currently, our best estimates of the size of contributing areas are based on topographic divides and fixed-width buffers.

[17] Lake-to-lake surface hydrologic connectivity was based on the stream network extracted from a hydrologically conditioned digital elevation model (DEM) (scale of 1:20,000). Using this stream network we classified lakes according to (1) a lake connectivity index [Martin and Soranno, 2006], (2) the Strahler order, and (3) a modified

Strahler order taking into account ephemeral and wetland connections [Riera *et al.*, 2000]. The lake connectivity index classified lakes into the following classes: isolated (no stream connections), outflow (only outflowing stream), and flow through (both inflowing and outflowing streams). The modified Strahler ordering differentiated between zero-order lakes with and without wetland connections to other lakes or streams. All three measures of lake-to-lake connectivity were based on potential connections derived from digital terrain information and did not take into account the temporal dynamics of the system.

[18] Groundwater connectivity was assessed with the purpose of assigning lakes to shorter- versus longer-flow systems (Table 1). Ca + Mg (mg L^{-1}) was used as a lake-based chemical indicator of groundwater flow length. One Ca + Mg measurement was made in each lake either during August of 1998, 1999, or 2001. We made the assumption that interannual variability in Ca + Mg would be small compared to lake-to-lake variability. Analysis of variance at a subset of lakes ($n = 5$) confirmed that of the total variation in Ca + Mg only 3% was due to differences in years, whereas 76% of the total variation in Ca + Mg was due to interlake differences.

3.2. Trophic Status

[19] The indicator of trophic status was based on the concentration of surface chlorophyll *a* as derived from satellite images ($(\text{Chl } a)_{\text{sat}}$) over a period of 20 years. $(\text{Chl } a)_{\text{sat}}$ was derived by transforming normalized exoatmospheric reflectance to Chl *a* using a regression model developed from coincident ground and satellite-based data. A complete description of the methodology can be found in work by Sass *et al.* [2007]. The following is a brief summary of this methodology.

[20] 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 end of summer period from late July to late August, and (2) the image had no or minimal cloud and haze. We used images acquired during the period from late July to late August, as this is the period when algal production generally peaks [Bayley *et al.*, 2007]. In the companion paper [Sass *et al.*, 2008] we showed using a supplementary data set that lake-based Chl *a* variability within August was much smaller ($\approx 15\%$) than the interannual variability ($\approx 85\%$), suggesting that images captured anytime during this period can be used to characterize end of summer algal production. However, since we were unable to perform a similar comparison with our Chl *a* data set, the dominance of interannual variability over intra-annual variability remains a critical assumption. Landsat TM band 3 images (one for each year between 1984 and 2003 except for 1992, 1995, 1996) were georectified and radiometrically normalized using a pseudoinvariant features correction method [Kloiber *et al.*, 2002], creating images with exoatmospheric reflectance (%) at 25 m pixel resolution. A 3×3 window (9 pixels) at the center of each lake was used to extract an average reflectance value comprising the satellite-based sample of Chl *a*. To minimize satellite signal contamination, some lakes were excluded from the analysis: (1) lakes with areas less than 5 ha were excluded to avoid errors resulting from “mixed” pixels that combined lake and shoreline; (2) lakes with standard deviation >

2 (%) were removed 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 band 5 and therefore water alone would have a small standard deviation); and (3) lakes with cloud or haze cover were excluded.

[21] Coincident ground-based Chl *a* data were available for 1999, 2001, 2002, which were used to calibrate (2001; $n = 18$) and validate (1999 and 2002; $n = 8$) a simple linear regression model [Sass *et al.*, 2007]. Lakes were surveyed at their center by taking a grab sample at 0.2–0.4 m depth. The linear regression equation ($R^2 = 0.68$, $p < 0.0001$, $\text{SE} = 0.65$, $n = 18$) was used to convert exoatmospheric reflectance to $(\text{Chl } a)_{\text{sat}}$ for all available imagery between 1984 and 2003. We performed all analyses on natural logarithm transformed data because of nonnormality of Chl *a*. To explore the spatial variation in $(\text{Chl } a)_{\text{sat}}$, we computed a long-term median of $(\text{Chl } a)_{\text{sat}}$ ($\text{med}(\text{Chl } a)_{\text{sat}}$) ($n_{\text{year}} = 17$) for each available lake ($n_{\text{lake}} = 40$). We compared $\text{med}(\text{Chl } a)_{\text{sat}}$ computed for all 17 years with $\text{med}(\text{Chl } a)_{\text{sat}}$ computed for only the years with available microwave imagery used to derive wetland areas and found no statistical difference (Kolmogorov-Smirnov $Z = 0.78$, $p = 0.57$). We assumed that our estimate of Chl *a*, collected in the top 0.4 m of the water column was representative of Chl *a* over the entire water column. We felt this was a reasonable assumption given that these shallow lakes are well mixed. Lakes with severe blooms were probably an exception to this. We also assumed that species composition differences between lakes would be small. Most lakes are dominated by cyanobacteria by the end of the summer, specifically *Chroococcus* and *Microcystis* species (S. Bayley, unpublished data, 2001).

[22] We used a Monte Carlo approach to assess the effect of error in estimating Chl *a* from satellite reflectance for each lake for the 17-year period data set. We took the standard error of the regression model used to predict Chl *a* for each individual lake and added it as white noise to each lake estimate (we randomly sampled from a normal distribution centered on the original predicted value with the standard deviation equal to the standard error). To simulate the effect of misaligned radiometric correction between images, we further added a randomly sampled constant to each lake Chl *a* for a given year. The constant for a given year was based on random sampling of a normal distribution with zero mean and a standard deviation equal to the standard deviation of $(\text{Chl } a)_{\text{sat}}$ of pseudoinvariant features that were used to assess the temporal stability of images [Sass *et al.*, 2007]. We generated 1000 realizations of $\text{med}(\text{Chl } a)_{\text{sat}}$ and computed the coefficient of variation (CV) to use as an assessment of uncertainty.

3.3. Quantifying the Spatial Sources of Natural Variation in Trophic Status Using Regression Trees

[23] We used regression trees to explore and to quantify landscape controls on the spatial variation in trophic status. Regression trees are used in environmental problems where nonparametric variables or nonlinear interactions make parametric regression inappropriate [De'ath and Fabricius, 2000]. Regression trees also provide the advantage of allowing nominal or ordinal variables to be included as independent variables. We used the ANOVA method to iteratively partition the data set. Optimal tree size was determined by applying a tenfold cross validation and

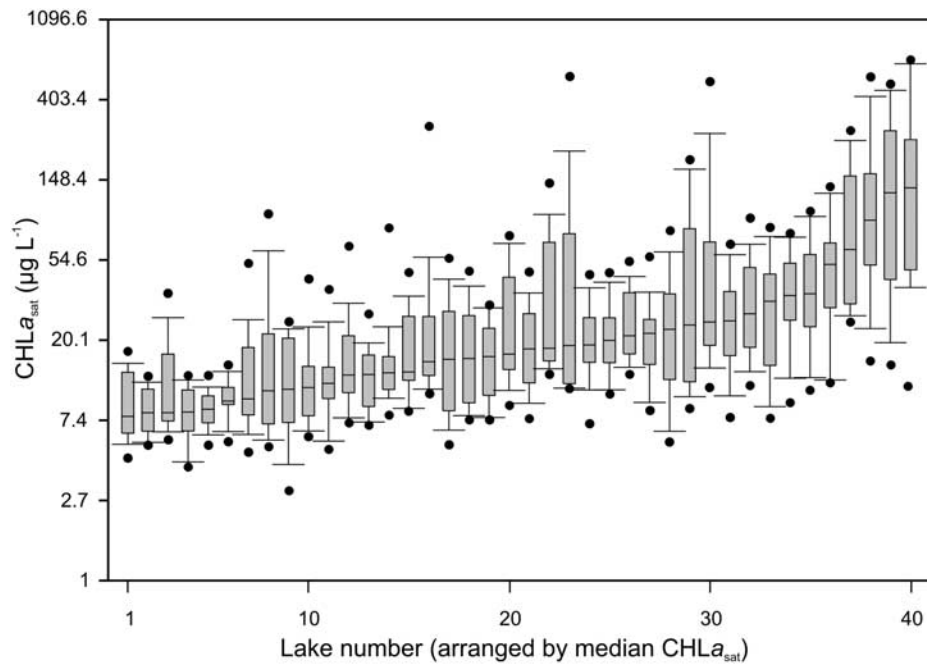


Figure 3. Distribution of satellite-based lake Chl *a* showing interannual variability across the forty study lakes. (Note: *y* axis labels were back transformed using exponential function.)

selecting the tree whose estimated cross-validation error was within one standard deviation of the minimum cross-validation error [Breiman *et al.*, 1984]. We used RPART implemented in SPLUS 4.0 to develop the regression trees [Therneau and Atkinson, 1997].

4. Results

[24] Significant lake-to-lake differences were observed in the statistical distribution of lake trophic status even after factoring in interannual variability (Figure 3), and $med(\text{Chl } a)_{\text{sat}}$ ranged from approximately $7 \mu\text{g L}^{-1}$ to almost $150 \mu\text{g L}^{-1}$ (Figure 3). A Kruskal-Wallis one-way analysis of variance on ranks showed significant differences in mean ranks among lakes ($H = 304.95, df = 40, p < 0.001$). The uncertainty analysis revealed that on average, the

$med(\text{Chl } a)_{\text{sat}}$ were 11% uncertain on the basis of the random errors added to the original data set. A more robust analysis of error would have compared long-term Chl *a* generated from in situ observation to the remote sensing estimates. However, rarely are these long-term measurements of trophic status available for lakes in this region.

[25] The final pruned regression tree explained 72% of the variance in trophic status as estimated by $med(\text{Chl } a)_{\text{sat}}$ (Figure 4). There were three statistically significant splits in the model where each split was based on a different independent measure of hydrologic connectivity. The most important split was based on Ca + Mg, which explained 54% of the total variation (Figure 4). Contrary to our expectation there was a positive correlation between Ca + Mg and $med(\text{Chl } a)_{\text{sat}}$, where lakes with Ca + Mg < 65.2 mg

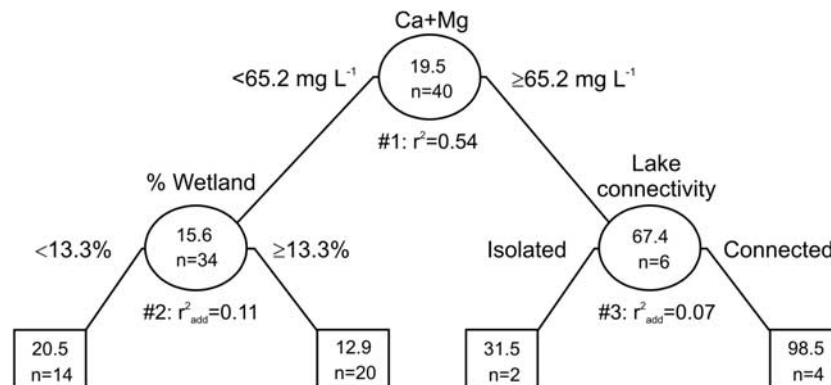


Figure 4. Regression tree predictions for long-term median in $(\text{Chl } a)_{\text{sat}}$. The model explained 72% of the total variance in $(\text{Chl } a)_{\text{sat}}$ (r^2_{add} values represent additional amount of variance explained). Ovals and rectangles represent splitting and terminal nodes, respectively. Numbers within node symbols indicate average $(\text{Chl } a)_{\text{sat}}$ ($\mu\text{g L}^{-1}$) (back transformed using exponential function) and sample size of that node.

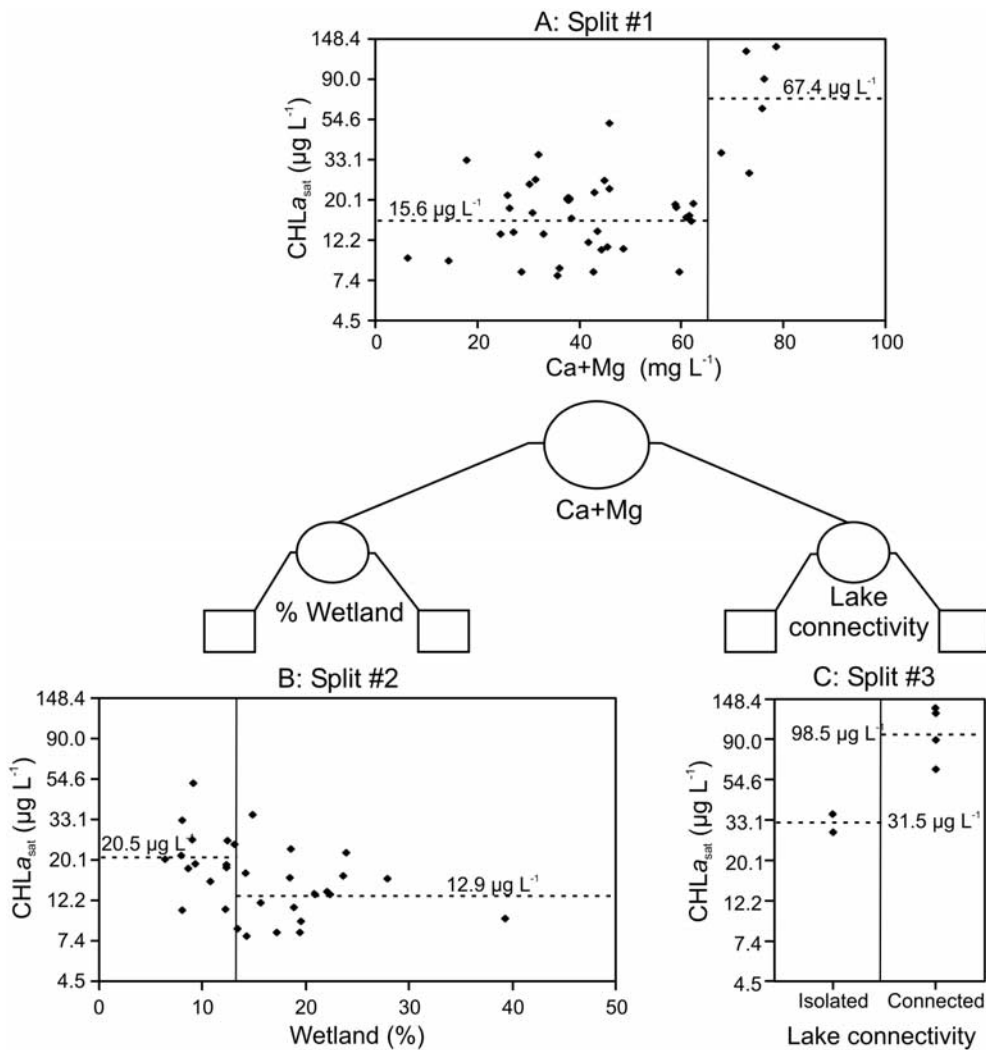


Figure 5. Hydrologic influence on the spatial variation in long-term median of $(\text{Chl } a)_{\text{sat}}$ as measured by (a) $\text{Ca} + \text{Mg}$, (b) percent wetland cover within watershed, and (c) lake connectivity through streams. For each scatterplot, vertical solid line represents the splitting threshold of the independent variable and horizontal dashed lines represent the two responses in the dependent variable of the regression model shown in Figure 4. (Note: y axis labels were back transformed using exponential function.)

L^{-1} experienced lower $\text{med}(\text{Chl } a)_{\text{sat}}$ ($15.6 \mu\text{g L}^{-1}$) than lakes with $\text{Ca} + \text{Mg} \geq 65.2 \text{ mg L}^{-1}$, which experienced significantly higher $\text{med}(\text{Chl } a)_{\text{sat}}$ ($67.4 \mu\text{g L}^{-1}$) (Figure 5a). The second most important split was based on %Wet, which explained a further 11% of the total variation (Figure 4). This split was made on the $\text{Ca} + \text{Mg} < 65.2 \text{ mg L}^{-1}$ side of the tree, which included a majority (85%) of the study lakes. Within this branch, %Wet had a negative effect on $\text{med}(\text{Chl } a)_{\text{sat}}$, where higher %Wet ($\geq 13.3\%$) resulted in lower $\text{med}(\text{Chl } a)_{\text{sat}}$ ($12.9 \mu\text{g L}^{-1}$) and lower %Wet ($< 13.3\%$) resulted in higher $\text{med}(\text{Chl } a)_{\text{sat}}$ ($20.5 \mu\text{g L}^{-1}$) (Figure 5b). The last significant split was based on lake connectivity through streams on the $\text{Ca} + \text{Mg} \geq 65.2 \text{ mg L}^{-1}$ side of the regression tree. This branch accounted for 15% ($n = 6$) of the lakes in the data set. Lake connectivity explained a further 7% of the total variation in $\text{med}(\text{Chl } a)_{\text{sat}}$. Within this branch, isolated lakes exhibited lower $\text{med}(\text{Chl } a)_{\text{sat}}$ ($31.5 \mu\text{g L}^{-1}$) than connected lakes ($98.5 \mu\text{g L}^{-1}$) (Figure 5c). In the discussion we

explore potential biogeochemical mechanisms that may be responsible for the observed pattern in the spatial variation of $\text{med}(\text{Chl } a)_{\text{sat}}$.

5. Discussion

[26] Herein we discuss the observed hydroecological patterns, compare the observed patterns with the expected patterns and provide possible biogeochemical explanations for the differences. We have structured the discussion on the potential hydrological controls on trophic status to reflect the hierarchy of explanatory variables of the regression tree. An underlying assumption to these biogeochemical inferences is that the metrics of hydrological connectivity we employ represent real hydrological processes (e.g., % wetland cover of a watershed represents the contributing area from which saturated overland flow is the dominant hydrological transport mechanism).

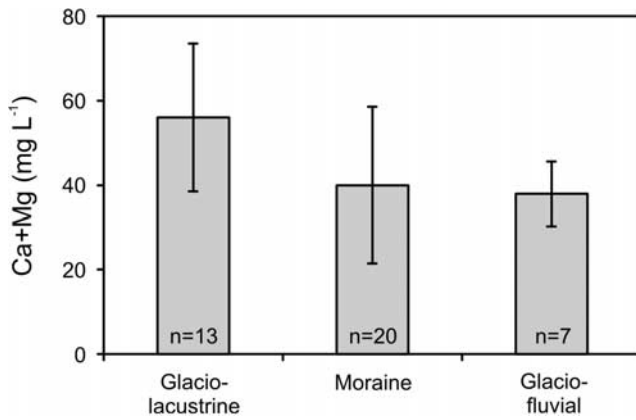


Figure 6. Bar graphs showing difference in means of Ca + Mg between the three dominant glacial landform units. Whiskers depict ± 1 standard deviation around mean.

5.1. Groundwater Controls on Trophic Status

[27] Ca + Mg was the hydrologic metric that explained the highest percentage of variance in $med(\text{Chl } a)_{\text{sat}}$ (Figure 4). Contrary to our expectation (Table 1), lakes with higher Ca + Mg exhibited higher $med(\text{Chl } a)_{\text{sat}}$. We expected lakes with higher Ca + Mg, and by proxy longer flow paths, to have lower $med(\text{Chl } a)_{\text{sat}}$ since phosphorus (P), the limiting nutrient to algal growth is highly adsorbed by clay particles [Evans et al., 2000; Macrae et al., 2005]. This expectation was supported by work in another part of the Boreal Plain with similar physiographic setting where lakes with higher Ca + Mg showed much smaller changes in P from 1 year to the next possibly because of increased influence of low P water discharging from longer groundwater flow paths [Devito et al., 2000].

[28] We offer two alternative hypotheses in explaining the observed trends. One possible explanation is that Ca + Mg is a valid proxy for flow path length, however, the P content of the groundwater does not have a big influence on lake water P content. Rather flow path length is related to P gradients across the sediment/water column interface. As most lakes on the Boreal Plain have P rich sediments [Prepas et al., 2001], we can assume that similar amounts of P are available in the sediments of all lakes. However, there can be large differences in the way lakes interact with the groundwater system. Groundwater reversals are commonly observed on this subhumid landscape but with differences in frequency and duration based on landscape position [Ferone and Devito, 2004]. Therefore, we propose that in lakes where hydraulic gradients are positive, more P (from sediment) is moved into the water column than in lakes where hydraulic gradients are negative. This type of groundwater driven P loading was postulated as a likely mechanism to account for internal loading rates of P in a lake on the Boreal Plain [Shaw et al., 1990].

[29] Another explanation for the trend observed in the first split of the regression tree is that in these lakes Ca + Mg is more a reflection of the geochemical nature of the substrate in the drainage basin. There was evidence for this as five of six lakes with $\text{Ca} + \text{Mg} \geq 65.2 \text{ mg L}^{-1}$ were located on the glaciolacustrine clay plain. A one-way analysis of variance showed a significant difference in

Ca + Mg between the three dominant surficial geological units ($F = 4.24$; $p < 0.05$) with the clay plain lakes having higher mean Ca + Mg (56.0 mg L^{-1}) than lakes located on the moraine (39.9 mg L^{-1}) and glaciofluvial outwash plain (37.9 mg L^{-1}) (Figure 6). The geochemical explanation may simply imply that the clay plain is richer in both Ca + Mg and P. Alternatively, the high Ca + Mg signal in the clay plain lakes might imply a much more efficient horizontal transport of P laden surface water from P-rich wetlands and uplands to lakes because clay plain catchments have very low hydraulic conductivity clays that favor surface runoff. We further explored the importance of surficial geology in explaining spatial heterogeneity in trophic status by replacing Ca + Mg with surficial geology in the regression tree. Surficial geology was not a significant predictor in the resulting tree. This suggests that Ca + Mg reflected not only a geochemical signal embedded in the surficial geology but possibly some other physical attribute of the drainage basin.

5.2. Surface Water Controls on Trophic Status

[30] The second and third splits of the regression tree (Figure 4) both indicated the importance of surface water connectivity (i.e., saturated overland flow and streamflow) on explaining the spatial variation of lake trophic status. In lakes with lower Ca + Mg, %Wet was the most important explanatory variable. The response of Chl *a* based on the split in %Wet was negative: lakes exhibited lower $med(\text{Chl } a)_{\text{sat}}$ when surrounded by a higher percentage of wetlands (Figure 5b).

[31] A negative relation between %Wet and $med(\text{Chl } a)_{\text{sat}}$ was contrary to our expectation as we expected wetlands to be a source of P (Table 1). Other studies on the Boreal Plain [Devito et al., 2000] and elsewhere [Dillon et al., 1991; Dillon and Molot, 1997; D'Arcy and Carignan, 1997] have shown that %Wet is positively associated with either P export from drainage basins to lakes or P concentrations measured in lakes. The mechanism responsible for this positive trend is the mobilization and transport of P from wetlands to receiving waters during wet, anoxic conditions [Evans et al., 2000]. Therefore, the bigger the wetland per unit drainage area, the more P will be transported. However, we found the opposite effect such that lakes with a larger wetland surrounding them had lower $med(\text{Chl } a)_{\text{sat}}$.

[32] One explanation for the observed pattern is that the P loading effects were overwhelmed by water volume effects leading to dilution of P and Chl *a* (i.e., despite large loadings of P from larger wetlands, larger wetlands also produced larger water outputs). Currently, we know that wetlands are an important source of water during wet periods [Ferone and Devito, 2004]. However, we lack data that would support a negative correlation between nutrient flux and wetland cover. Other studies have documented negative correlations between hydrologic metrics (such as discharge, precipitation, or water depth) and indicators of trophic status [Duarte and Kalff, 1986; Noges et al., 2003; Markensten, 2006; Sass et al., 2008] suggesting that the dilution of P and Chl *a* might be a more prevalent mechanism than previously thought. Most of these studies have focused on the temporal variation of trophic status, however, it is likely that similar dilution effects are present when looking at the spatial distribution of hydrologic contributing areas.

[33] An alternative explanation for the observed pattern is that wetlands act as filters. A sequestering mechanism was suggested by *Prepas et al.* [2001], who also found a negative correlation between percent wetland and total P in 26 lakes on the Boreal Plain. However, *Prepas et al.* [2001] also found an inflection point where in basins with wetland percentages exceeding 50% the response between wetland coverage and total P was positive. They suggested that in basins where wetland coverage was less than 50%, rich fens dominated and they acted as P sequesters, whereas in basins where wetland coverage was greater than 50%, wetlands (dominated by bogs) acted as P conveyors. Our data set (Figure 5b) did not show a similar inflection point.

[34] In lakes with higher Ca + Mg ($\geq 65.2 \text{ mg L}^{-1}$), lake connectivity was the most important explanatory variable. The split based on lake connectivity separated those lakes that were isolated from lakes that were integrated into the stream network. The position of the node for lake connectivity on the regression tree makes intuitive sense as lakes lower in the landscape have not only higher proportion of longer groundwater flow paths (higher Ca + Mg) but also these lakes have the potential for greater lake-to-lake connectivity. Lakes had higher $(\text{Chl } a)_{\text{sat}}$ when connected to other lakes. Although streamflow is generally intermittent in most low-order streams on the Boreal Plain [*Munn and Prepas*, 1986], P export can be substantial when there is discharge [*Cooke and Prepas*, 1998]. The four connected study lakes were all flow-through lakes suggesting that there was a net gain in P in all of them. It is possible that in some flow-through lakes P leaving the lake is greater than P entering a lake and thereby having an overall net loss.

[35] Overall, these results suggest that hydrology plays an important role in controlling the long-term trophic status of lakes in this part of the Boreal Plain. Although some of the observed patterns seem counterintuitive to previous studies, they might reflect the fact that this study was based on a spatially and temporally extensive database, while previous studies [e.g., *Devito et al.*, 2000] were not. Spatially and temporally extensive data sets, often based on remote sensing technology, are allowing new insights into hydrological, biogeochemical, and ecological patterns [e.g., *Sobek et al.*, 2007]. It is not unreasonable to expect different patterns emerge when the spatial and temporal extents are enlarged since this captures more of the range in natural variation. However, as our study shows, the challenge of inferring process from pattern remains. Our study offers clues as to which direction future process studies should progress.

6. Conclusions

[36] In this study we used regression tree analysis to identify the major sources of spatial heterogeneity in the concentration of long-term median of summer chlorophyll *a* in shallow lakes on the Boreal Plain. We found that simple hydrologic metrics were able to explain 72% of the spatial variation in $\text{med}(\text{Chl } a)_{\text{sat}}$ as estimated by satellite imagery. The nature of the relations between hydrologic controls and trophic status revealed unexpected patterns. We interpreted the patterns by assuming that the hydrological metrics were influencing trophic status through a positive and linear correlation between phosphorus and Chl *a*. There was a positive relation between $\text{med}(\text{Chl } a)_{\text{sat}}$ and Ca + Mg suggesting either that (1) where Ca + Mg is higher

experience water discharge which drives P loading from sediments, or (2) lakes where Ca + Mg is higher reflect a geologic substrate with higher P availability. The majority of the study lakes belonged to the group of lakes with lower Ca + Mg. Within this group of lakes, wetlands played an important role in regulating trophic status. Contrary to expectation, percent wetland coverage was negatively related to trophic status, which most likely reflected a dilution effect due to proportionately higher runoff ratios in lakes with larger wetlands. For the minority of study lakes with higher Ca + Mg, trophic status was further enhanced in lakes that were connected to other lakes, most likely a direct result of stream P transport. These results highlight the importance of considering hydrologic dynamics when understanding differences in trophic status. Future work is needed to investigate the processes responsible for the trends detected here. A better understanding of the physical and biological controls on the natural variation in trophic status of lakes will lead to more effective management strategies that try to mitigate the anthropogenic impacts on aquatic systems on the Boreal Plain.

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