Cyanobacteria in North America: Modelling across nutrient and temperature gradients

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A lake is the landscape's most beautiful and expressive feature. It is earth's eye; looking into which the beholder measures the depth of his own nature. –Henry David Thoreau

Abstract

The toxin-producing potential of some freshwater cyanobacterial species and their ability to form dense blooms makes the possibility of an increase in their biomass of concern to lake managers and the general public. Modelling of cyanobacterial biomass and dominance in inland water bodies has demonstrated that cyanobacterial biomass increases concomitantly with nutrients in freshwater systems. Though temperature and water-column stratification are increasingly cited as factors promoting cyanobacterial biomass, support for this has been mainly provided by laboratory studies and individual lake studies. Furthermore it is not well known if models developed across large spatial gradients perform adequately at regional scales where responses could be modulated by additional unconsidered regionally-distinct variables. This thesis evaluates the effects of temperature, nutrients and other predictors on cyanobacterial biomass in North American lakes, through general models and when accounting for water body type and region of origin.

A novel analysis of an existing dataset comprising single sample dates of over 1000 lakes in the United States showed that temperature was a significant predictor of cyanobacterial biomass. The effect of temperature was shown to be independent of those of nutrients and increases in total phytoplankton biomass. This suggests that warming alone might result in an increase in cyanobacterial biomass in lakes. The effects of the different variables varied between the lake systems considered (deep or shallow; natural lake or reservoir) with the strongest relationships found in deep natural lakes.

An unpublished dataset of 88 Canadian lakes was used to test the effects of nutrients and temperature across regions using seasonally averaged data. These robust models provide some support for differing responses among regions, suggesting caution when applying general models to specific regions. Additionally, cyanobacterial genera biomass distribution in lakes was found to be explained by multiple environmental variables.

Generally, nitrogen was found to be a significantly better predictor of cyanobacterial biomass than total phosphorus suggesting that nitrogen-fixation by cyanobacteria is less prevalent that previously estimated. Together, this thesis advances our understanding of the variables driving cyanobacterial biomass in lakes and demonstrates that under continued nutrient enrichment and warming temperatures increases in cyanobacterial biomasses in North American lakes could be expected.

Sommaire

Les proliférations de cyanobactéries sont des sujets de préoccupation à l'échelle globale en raison de leur capacité de former des écumes denses qui épuisent l'oxygène dissoute et qui peuvent produire des toxines, nuisant à l'utilisation des plans d'eau tant pour l'eau potable que les loisirs. La modélisation de la biomasse et de la dominance des cyanobactéries a préalablement démontré que leur abondance augmente de façon concomitante avec les nutriments dans les systèmes d'eau douce. Bien que la température et la stratification de la colonne d'eau soient de plus en plus citées comme facteurs favorisant la prolifération des cyanobactéries, ces associations sont surtout basées sur des études en laboratoire et de lacs individuels. En outre, il n'a pas été bien démontré que les modèles développés sur d'importants gradients spatiaux s'appliquent de façon adéquate à l'échelle régionale, où la biomasse pourrait aussi être modulée par des variables additionnels. Cette thèse évalue les effets de la température, des nutriments et d'autres prédicteurs sur la biomasse des cyanobactéries dans les lacs d'Amérique du Nord, à travers le développement de modèles général ainsi que des modèles tenant compte des spécificités régionales.

Dans le premier chapitre, je présente une analyse exhaustive d'un ensemble de données de plus de 1000 lacs. Utilisant cet ensemble de données, où la plupart des lacs ont été échantillonnés une seule fois au cours de la saison de croissance, j'ai démontré que les concentrations de nutriments (azote et phosphore) et la température étaient des prédicteurs significatifs de la biomasse des cyanobactéries. L'effet de la température sur la biomasse des cyanobactéries

est statistiquement indépendant de celui des nutriments. Ces résultats suggèrent que le réchauffement des eaux de surface pourrait entraîner une augmentation de la biomasse des cyanobactéries dans les lacs. Les effets des variables différaient entre les systèmes étudies (profonds, peu profond ; lac naturel, réservoir). Les meilleurs modèles ont été développés pour lacs naturels profonds.

Dans le deuxième chapitre de cette thèse, j'ai examiné un ensemble de données inédites basées sur les moyennes saisonnières de 88 lacs provenant de trois régions du Canada (l'Alberta, la Colombie-Britannique et l'Ontario). J'ai développé des modèles prédictifs généraux et examiné comment les modèles pouvaient différer entre les régions en utilisant la modélisation linéaire générale et la modélisation à effets mixtes. Les prédicteurs environnementaux ressortant furent similaires à ceux du premier chapitre mais, tel qu'attendu, les modèles utilisant les moyennes saisonnières expliquèrent une plus grande proportion de la variance de la biomasse des cyanobactéries car elles sont plus représentatives. Ces modèles ont aussi relevé des différences claires entre l'Ontario et les autres provinces mais l'inclusion d'avantage de lacs de l'Ontario dans l'analyse serait nécessaire afin de résoudre pourquoi c'est le cas.

Dans l'ensemble, cette thèse enrichit notre compréhension des variables influençant la prolifération des cyanobactéries dans les lacs. Elle démontre clairement que, par l'enrichissement continu en nutriments et le réchauffement des eaux de surface, une augmentation de la biomasse des cyanobactéries dans les lacs nord-américains serait attendue.

Preface

This thesis was prepared in accordance with the Faculty of Graduate and Postdoctoral Studies Office's "Thesis Submission Guidelines" and completed under the supervision of Dr. Irene Gregory-Eaves at McGill University and Dr. Frances R. Pick at the University of Ottawa. Funding for this research was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), Hydro-Québec and McGill University. Both chapters were prepared with the intention for publication in peer-reviewed journals. Dr. Irene Gregory-Eaves, Dr. Frances R. Pick and I collaborated to develop the ideas and the interpretations found in this thesis. I conducted all treatment and statistical analysis of data.

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General Introduction

Cultural eutrophication of surface waters is a major stressor affecting numerous ecosystems (Smith and Schindler 2009) and one that will likely increase in intensity with the rising demand for food (Tilman et al. 2001). Increases in algal biomass that occur as a result of nutrient pollution can impair aquatic ecosystem functions and the services they provide such as drinking water, recreational opportunities and fishery resources. Whereas many phytoplankton taxa are capable of forming blooms, the most notorious of these are the cyanobacteria. Dense cyanobacteria blooms can reduce light penetration in the water column, can cause oxygen-depletion and can produce odour problems through the production of geosmin and other metabolites. Some cyanobacteria also produce harmful toxins such as microcystins and anatoxins that have caused livestock deaths and human illness (Hitzfeld et al. 2000). Cyanobacteria blooms are increasingly reported in Canadian lakes, which is of considerable concern to lake managers and users (Kotak and Zurawell 2007; Winter et al. 2011).

Eutrophic lakes are most prone to cyanobacteria blooms and lake-water phosphorus concentrations are often considered to be the primary driver of such blooms (e.g. Håkanson et al. 2007). Lake-water phosphorus concentrations, in turn, are reflective of watershed soils, lake morphometry and human activities (e.g. waste water and agricultural inputs as well as land-cover changes). Cyanobacteria are capable of sequestering excess phosphorus allowing them to outcompete other faster growing algae under nutrient-poor conditions (i.e. a process commonly referred to as luxury consumption; reviewed by Carey et al.

2012). In addition to this strategy, cyanobacteria thrive at high nutrient concentrations where, as phytoplankton biomass increases, they outcompete eukaryotic algae for other limiting resources such as light and carbon dioxide (Havens et al. 2003; Shapiro 1997). Furthermore, at high phosphorus concentrations nitrogen limitation of algal biomass arises (Downing et al. 2001). Many species of cyanobacteria are thought to be competitive under these conditions because they are capable of nitrogen fixation, which releases them from nitrogen limitation.

Current models predicting cyanobacterial biomass and dominance from lake survey data focus almost exclusively on nutrient concentrations (such as total phosphorus and to a lesser extent total nitrogen) and are capable of explaining ~50% of the variation of cyanobacteria in lakes and estuaries (Trimbee and Prepas 1987; Downing et al. 2001; Håkanson et al. 2007). However, nutrient-based models fail to explain why cyanobacterial bloom occurrences are increasingly observed in oligo-mesotrophic lakes, which show interannual variability that does not occur with commensurate nutrient changes (Leblanc et al. 2008). Increasingly, scientists are quantifying the importance of temperature and related factors (i.e. strength of stratification) as predictors for cyanobacteria blooms (Jöhnk et al. 2008; Wagner and Adrian 2009; Kosten et al. 2012, Taranu et al. 2012). To date, the number of empirical studies linking climate changes to cyanobacterial biomass remains small relative to lab experiments and qualitative observations. As such, there is a need to further refine our understanding of how anticipated changes in climate will impact freshwater systems and the services

they provide us.

A number of traits found within the cyanobacterial phylum provide them with advantages under warmer conditions. For example, a synthesis of experimental data shows that cyanobacteria growth is favoured under warm temperatures, as species maximum growth rates are generally reached at higher temperatures (~25°C) relative to eukaryotic phytoplankton (Robarts and Zohary 1987). A prolonged growing season with warmer temperatures could also allow cyanobacterial species to attain greater total biomasses. Furthermore, increased lake stratification under warming conditions is an indirect effect of temperature thought to favour cyanobacteria. The presence of vacuoles in many of these species allows for motility in the water column, whereas heavier algal cells like diatoms may sink out of the photic zone. In stratified water columns buoyancy-regulating cyanobacterial species are capable of sequentially harvesting light in the epilimnion and then migrating to the hypolimnion where they can uptake a more plentiful supply of nutrients. Increased strength and duration of stratification under warming conditions might be specifically advantageous to genera that migrate rapidly through the water column such as *Microcystis* and *Anabaena* (Carey et al. 2012). Furthermore, by forming dense surface mats, cyanobacteria can contribute to the warming and stratification of the water-column by absorbing heat in the uppermost layer (Rinke et al. 2010). Together, these traits suggest that environmental conditions such as water column stratification and high temperatures could be important drivers of cyanobacterial biomass and dominance.

Cyanobacteria, like other phytoplankton groups, can be categorized into functional groups based on their eco-physiological traits and broad distribution (Reynolds 1984; Reynolds et al. 2002; Litchman et al. 2007). For example, planktonic cyanobacteria can be divided into species capable of fixing gaseous di-nitrogen, those capable of regulating their buoyancy and colonial species (Dokulil and Teubner 2000). In addition, we can categorize taxa according to whether or not they have the potential to produce hepato- or neurotoxins. By grouping cyanobacteria genera from the data-set within these groups it should be possible to test whether the biomass and dominance of specific eco-types in the water-column can be predicted by key environmental factors. Predictive factors such as nutrients, temperature and water-column stratification would be expected to have variable effects on cyanobacterial species depending on their respective physiological optimums and specific adaptations.

Cyanobacterial modelling has been underway for some time, but to date there has been little attention paid to how different model types affect our ability to predict cyanobacterial biomass in a given lake. For example, across different regions, a number of factors could vary that would bring about significant differences in cyanobacteria and thus applying models from one region to another would lead to serious under or overestimates. Factors that could vary regionally include 1) differences in other environmental variables (e.g. pH and conductivity) that could modify cyanobacteria response to nutrients and temperature-related variables, 2) differences in the range of nutrients and temperature-related variables as Downing et al. (2001) has shown that the relationship between nutrients and

cyanobacteria dominance is non-linear and 3) differences in community composition of cyanobacteria. Identifying whether regional models differ and determining whether model fit is stronger at the regional vs. continental scale is of particular importance to managers who are working at a watershed or regional scale. Here they want to know if existing predictive models are likely to be successful in an area for which they may not have any or only very limited data

Thesis objectives

The objectives of my thesis were to quantify the effect of temperature and other environmental variables in promoting cyanobacterial biomass in North American lakes and test whether these effects varied across regions and lake-system types. The goal of the first chapter was to empirically model cyanobacterial biomass using a very large (1000+) lake American dataset (i.e. the 2007 United States National Lake Assessment; herein referred to as the NLA dataset). Applying a variety of modelling approaches, I set out to quantify the proportion of variance in cyanobacterial biomass in the NLA dataset that could be attributed to temperature-related factors, as well as other environmental variables. I used the method of path analysis to test for indirect and direct effects of nutrients and temperature in promoting both algal (as estimated by chlorophyll *a*) and cyanobacterial biomass. Considering the data as binary subsets of lake types (deep vs shallow and natural lakes vs. reservoirs) allowed me to test for differences in models among waterbody types. Before I could take on these modelling procedures, however, I had to develop a conversion table for cyanobacterial

species and genera, which could allow investigators to convert cyanobacterial counts into biomass estimates.

One of the limitations of the NLA dataset was that most lakes were sampled once during the growing season in 2007. Given that cyanobacteria are inherently dynamic (Håkanson 2007), I set out in chapter two to develop predictive cyanobacterial biomass models using seasonally-integrated data from Canadian lakes. I also tested for differences in regional and continental-scale models using unpublished data from three provincial Ministries of the Environment (Alberta, British Columbia, and Ontario). I used linear modelling and mixed-effects models (an extension of general linear models that allows for random effects to vary between subsets of the data) to develop models and test whether there were significant differences among provinces. I also conducted a multivariate analysis to quantify the association between cyanobacterial genera with environmental variables. To my knowledge, this chapter represents the first attempt to develop predictive pan-Canadian models for cyanobacterial biomass.

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Nutrients and water temperature are significant predictors of cyanobacterial biomass in a ~1000 lake dataset

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Abstract

Using a ~1000-lake dataset that spans the entire continental U.S.A., we applied empirical modelling approaches to quantify the relative strength of nutrients and water temperature as predictors of cyanobacterial biomass. Given that cyanobacteria possess numerous traits providing competitive advantage under warmer conditions, we hypothesized that water temperature, in addition to nutrients, is a significant predictor of cyanobacterial biomass. Total nitrogen (TN), mean water column temperature and total phosphorus (TP) were all significant predictors of cyanobacterial biomass, explaining independently 17%, 13% and 12% of the variation based on a single epilimnetic sample per lake. TN and water temperature provided the best multiple regression model and explained 25% of the variance in cyanobacterial biomass. However, when the dataset was divided according to basin type, these same variables explained a higher amount of the variation in deep natural lakes (33%, n=253), whereas the least amount of variation was explained by these variables in shallow reservoirs (12%, n = 307). Competing path models on the full dataset using the best variables selected by multiple linear regression suggested that the effects of nitrogen on cyanobacteria was mediated through total algal biomass. In contrast, temperature showed both an indirect effect mediated through total algal biomass as well as direct effect on cyanobacterial biomass across all lake types. Under a scenario of atmospheric CO_2 doubling from 1990 levels (resulting in a 3.3ºC increase of the maximum lake surface water), we would predict on average a doubling of cyanobacterial biomass.

Globally, cyanobacterial blooms represent a key water quality concern. In numerous regions around the world, there has been a significant increase in the reporting of cyanobacterial blooms over the past few decades (Winter et al. 2011, O'Neil et al. 2012). Whereas some of this increase in reporting may be due to a growing societal awareness and changes in sampling effort, increases in phosphorus and nitrogen loading as well as climate change may be responsible for promoting the growth of cyanobacteria (e.g. Paerl and Huisman 2008). To date, empirical modelling has shown that both phosphorus and nitrogen are important drivers of cyanobacterial abundance and dominance (e.g. Pick and Lean 1987; Downing et al. 2001; Håkanson et al. 2007). Furthermore, temperature and related factors (e.g. strength of stratification) are increasingly recognized as important predictors of cyanobacterial biomass across spatial and temporal gradients (Jöhnk et al. 2008, Wagner and Adrian 2009; Kosten et al. 2012). However, the relative importance of phosphorus, nitrogen and temperature as predictors of cyanobacteria across a large range of lake morphometries has not been clearly defined.

Climatic warming is affecting temperate lakes by prolonging the duration of the open-water season, increasing water-residence times, and strengthening the stratification of the water column during the growing season (e.g. Kundzewicz et al. 2007, Schindler 2009). Cyanobacteria possess a number of traits that provide them with advantages under warmer conditions (Paerl and Paul 2012, but see Carey et al. 2012). For example, a synthesis of experimental data suggests that

cyanobacterial growth is favoured under warm temperatures, as species maximum growth rates are generally reached at higher temperatures (~25°C) relative to eukaryotic phytoplankton (Robarts and Zohary 1987, Paerl et al. 2011). A warmer, more stable water-column also favours cyanobacteria (e.g. Jöhnk et al. 2008), because the gas vacuoles of many planktonic species allows for motility in the water column and access to nutrients from the hypolimnion. Collectively, these traits suggest that environmental conditions such as water column stratification and high temperatures could be important drivers of cyanobacterial biomass and dominance.

Human activities have also fundamentally altered the nitrogen cycle by doubling the global fixation of reactive nitrogen (Galloway and Cowling 2002). The full consequence of this enhanced nitrogen loading on lakes is still very much under study but a meta-analysis of over 900 aquatic experiments has indicated that autotrophs are most likely to be both N and P limited in lakes (Elser et al. 2007). In particular, highly P enriched lakes may present signs of N limitation (Downing and McCauley 1992). Certainly our understanding of the role of nitrogen in influencing cyanobacterial biomass has changed considerably over the past few decades. The ability of some cyanobacteria to fix dinitrogen led to the proposition that the N:P ratio was an important predictor of cyanobacteria (Smith 1983), but subsequent empirical analyses have shown weak support for this model (Trimbee and Prepas 1987; Downing et al 2001).

We took advantage of a dataset representing over 1000 lakes to determine the strength of nutrients and temperature as predictors of cyanobacterial biomass.

The data analyzed were collected as part of the 2007 United States National Lakes Assessment (NLA) (USEPA, 2009). For this program lakes were selected to provide a statistically representative subsample of all continental US lakes larger than four hectares in surface area (USEPA, 2009). The large geographic span as well as the extensive nutrient and temperature gradients captured by the NLA dataset allowed us to test: a) the relative strength of phosphorus, nitrogen and temperature as predictors of cyanobacterial biomass in lakes of the U.S.A.; and b) whether including temperature in predictive cyanobacteria-nutrient models significantly improves the fit. We hypothesized based on the existing literature that water temperature, in addition to nutrient concentrations, would be significant predictors of cyanobacteria. We also applied a path analysis approach to identify whether the effect of temperature on cyanobacteria is direct, indirect or both. General lake types of shallow vs. stratified systems and natural lakes vs. reservoirs were further tested separately as morphometry and differences in water residence time are known to affect phytoplankton community structure (Kalff 2001). With this knowledge, the risks of cyanobacterial blooms can be assessed under a wide range of conditions.

Methods

National Lake assessment program - The 1147 lakes represented in the NLA dataset span large gradients in nutrients and temperature encompassing temperate, subtropical and alpine regions (Table 1). Following a standardized sampling protocol (USEPA 2006, 2007) all lakes were sampled once from early

May to mid-October of 2007. From the deepest point in each lake, sampling crews collected vertical temperature profiles at 1 m intervals (or 0.5 m intervals for lakes < 3 m) and integrated water samples from the uppermost 2 meters for water chemistry, phytoplankton and chlorophyll *a* analyses. For temperature effects we considered here both the surface temperature and the mean water column temperature (calculated from the depth profiles recorded). A single laboratory analyzed all water chemistry samples (USEPA 2009). Chlorophyll *a* was used as a proxy for total phytoplankton biomass. Detection limits for total phosphorus and total nitrogen were 4 μg L^{-1} and 20 μg L^{-1}, respectively.

The phycological component of the NLA dataset was processed by EcoAnalysts, Inc. according to USGS NAWQA methods (Charles et al. 2003). Picocyanobacteria were not enumerated. Quality control analysis of 10% of samples was performed by independent taxonomists (USEPA 2010). To account for discrepancies between analysts, some groups were combined to coarser taxonomic units to form the operational taxonomic units (generally aggregated to the genus level). Cell densities were calculated for all identified phytoplankton, but no size measurements were taken to determine biovolume. We therefore estimated average cell volumes for each cyanobacterial group using dimensions from taxonomic references (Cronberg and Annodotter 2006, Komárek and Anagnostidis 1998, 2008). Cell dimensions (ranges or fixed values) and simple cell volume equations (spherical, ovoid or cylindrical) were used to determine the cell volume range of a species (Hillebrand 1999). The median volume within this range was then used as the estimated cell volume for each taxon. For counts only

identified to the genus level (e.g. when species identification was not feasible), the median value of all the documented species within that genus was used to estimate cell biovolume. For each sample, total cyanobacterial biovolume was determined by summing the estimated biovolume for each taxon recorded. We then converted biovolume estimates into biomass assuming a specific gravity of 1 g cm^{-3}. In order to assess the validity of this approach, we applied the formulas for estimating cell volumes to an independent set of lake phytoplankton samples (unpublished data set from the Ministries of the Environment in British Columbia, Alberta and Ontario) where both cell abundance and biovolume (and biomass) for each taxon were reported. Based on data from three different regions (with three different analysts): There was a very strong relationship between estimated cyanobacterial biomass and measured biomass (r^2_{adj}=0.90; $p<0.001$), with the slope of the equation slightly greater than 1 (Fig. 1). In addition to considering total cyanobacterial biomass, we also considered separately bloom-forming, potentially toxic, heterocystous (Nostocales) and potentially N-fixing taxa using the functional classification of Cronberg and Annodotter (2006) and others.

Statistical Analysis - To quantify the strength of temperature and nutrients (total phosphorus (TP), total nitrogen (TN)) as predictors of cyanobacterial biomass, univariate general linear modelling (GLMs) and non-linear modelling using general additive models (GAM; Wood 2011) were conducted. Bayesian Information Criterion (BIC) and r^2_{adj} values were used to select the best models. In order to meet conditions of normality and homogeneity of variance in the residuals, cyanobacterial biomass and nutrient variables were log-transformed.

For some lakes, reported values of nutrients were below the detection limit; in these cases a value between zero and the detection limit was randomly chosen as these values were in the tail of the overall nutrient distribution. By contrast, the detection limit of cyanobacterial biomass was not reported. Given that there were few reports of biomass values at or below 0.01 μg L^{-1}, we assumed that samples with zero cyanobacterial biomass could have as much as 0.01 μg L^{-1}. As such, for samples with zero cyanobacterial biomass reported, we assigned random values of decreasing probability between 0 – 0.01 μg L^{-1} to follow the broader tail in the cyanobacterial biomass distribution.

We also applied multiple linear regressions using all-possible subset variable selection (Quinn & Keough 2002; Lumley 2009). Additional independent variables considered in previous models of cyanobacterial biomass (N:P ratio, chlorophyll *a*, lake area, lake depth, latitude, conductivity, pH, Secchi depth) were tested. Of this set of variables N:P ratio, chlorophyll *a*, lake area, lake depth and conductivity were log-transformed. Collinearity amongst these explanatory variables was tested using variance inflation factors (VIFs) (Quinn & Keough 2002, Heiberger 2011).

Given that a recent large lake survey (Kosten et al. 2012) focused on shallow lakes maximum depth was less than 6 m, we tested whether there was a significant difference in cyanobacterial response models between deep and shallow NLA lakes based on this cut-off depth. We also analyzed separately natural lakes and human-made reservoirs because water residence is much shorter in reservoirs and this has been shown to influence phytoplankton biomass and

composition independently of nutrients (Carvalho et al. 2011).

Path analysis was used to address the direct and indirect effects of predictor variables and to test different possible mechanisms of interactions (Shipley 2002, Fox et al 2012). Using the best variables selected by multiple linear regression, we constructed a fully saturated model decomposing relationships into direct and indirect effects, as well as unresolved relationships. After validating the saturated model, we constructed several competing alternative scenarios that we validated statistically using BIC the goodness-of-fit index (GIF). All statistics were performed and plotted using R (R Development Core Team 2012; Wickham 2009).

Results

Across the continental USA, the NLA lakes exhibited a wide variation in environmental variables (Fig. 2, Table 1). Total phosphorus (TP) ranged over four orders of magnitude and the temperature ranged almost five fold during the sampling period. The median NLA lake was mesotrophic by OECD criteria (Ryding and Rast 1994) and had a temperature of 21 °C. Surface water temperature and mean water column temperature were highly correlated with elevation (analysis not presented), but were not correlated with either TP or TN concentrations (Fig. 3). However TN and TP were significantly correlated ($r=0.80$; Fig. 3).

Similar to the pronounced environmental variation observed, cyanobacterial cell densities ranged substantially (0 - 4.98 x 10^9 cells L^{-1}; Table

1). Following the guidelines developed by the World Health Organization (WHO 2003), 20% of the NLA lakes represent a medium risk of cyanobacterial toxicity (i.e. 20 000 - 100 000 cells ml^{-1}). An additional 7% of the NLA lakes fall within the WHO's high risk of cyanobacterial toxicity category that would require beach closure (i.e. cell counts greater than 100 000 cells ml^{-1}). By converting the NLA cyanobacterial cell count data into biomass estimates based on our literature survey, we found that the median biomass was 349 μg L^{-1}. Across the 1121 lakes reporting cyanobacteria, bloom-forming and/or potentially toxic taxa were widespread (Table 1). The five most important genera (i.e. genera representing more than 65% of the cyanobacterial biomass in any one lake) were *Microcystis, Oscillatoria (Planktothrix), Anabaena, Chroococcus* and *Lyngbya* (presented in decreasing order of dominance).

Univariate linear models consistently outperformed non-linear models with respect to all the variables considered. The variable that explained the most variation in cyanobacterial biomass was TN (17%). Temperature (considering surface or averaged over the water column) explained less variation but surprisingly approximately the same amount of variation as TP. Overall, chlorophyll *a* was the best predictor of cyanobacterial biomass, explaining 28% of the variation in cyanobacterial biomass (Fig. 4). We also considered the ratio of N:P and sampling day of the year, but neither explained a significant proportion of the variation (N:P: r^2_{adj}=0.02 ; p-value<0.05; day of the year: r^2_{adj}=0.002 ; p-value= 0.07). In contrast to the cyanobacterial models, TN and TP explained an equal and much greater proportion of the variation in chlorophyll *a*, and

temperature variables were weaker predictors (Table 2).

The strongest multiple linear regression model for CBB, considering TN, TP, surface temperature, mean temperature, conductivity and pH as possible predictors, included only TN and surface temperature and explained a quarter of the variability (r^2_{adj}=0.25; Table 2) with weak multicollinearity (VIF= 1.02). When considering bloom-forming or potentially-toxic cyanobacteria as response variables, the models obtained were similar to the overall cyanobacterial models (Table 2). Separating the cyanobacterial biomass data into lakes vs. reservoirs and deep vs. shallow systems identified more pronounced differences in the strength of the models (Fig. 5, Table 3). The strongest models were found with the deep lake subset (n = 253) whereas the weakest arose with the shallow reservoir subset (n = 307).

Using the key variables identified in the multivariate analyses above (TN, surface water temperature, chlorophyll *a* and cyanobacterial biomass), we constructed a fully saturated path analysis model and considered three competing hypotheses: 1) nitrogen and temperature act indirectly (via chlorophyll *a*) on cyanobacterial biomass; 2) in addition to the indirect effects of nitrogen and temperature, nitrogen acts directly upon cyanobacterial biomass and 3) in addition to the indirect effects of nitrogen and temperature, temperature acts directly upon cyanobacterial biomass. The model with the strongest support based on BIC and adjusted goodness of fit indices showed that temperature acts both directly and indirectly (via chlorophyll *a*) in predicting cyanobacterial biomass (Fig. 6). Interestingly, the effect of nitrogen was mainly mediated through that of

chlorophyll *a*.

Discussion

Based on this analysis of a large dataset spanning the continental U.S.A., we provide further evidence that total nutrients are a significant predictor of cyanobacterial biomass in lakes, total nitrogen in particular being a stronger statistical predictor of cyanobacterial biomass than total phosphorus. We also found support for the hypothesis that water temperature is a significant and independent predictor of cyanobacterial biomass. Our path analysis further demonstrates that the effect of temperature on cyanobacterial biomass is both direct and indirect whereas that of nutrients is mediated by total phytoplankton biomass (as estimated by chlorophyll *a*). Considering that almost 30% of lakes in the continental U.S.A. fall within the WHO medium-high risk categories for human and wildlife health, these results are pertinent for the management of numerous lakes in this region, and possibly to temperate lakes worldwide.

The management of temperate lakes for mitigating eutrophication has long focused on phosphorus control (Lewis et al. 2011), but our results suggest that this approach may be insufficient if the goal of these management efforts is to mitigate cyanobacterial growth and dominance. In particular, our results provide support for the models based on smaller data sets (~ 100 lakes; Downing et al. 2001 ; Håkanson et al. 2007 ; Dolman et al. 2012), which have also shown that nitrogen is generally a stronger predictor of cyanobacterial biomass and dominance than phosphorus and that the ratio of these nutrients generally providing weaker

models. However, in other regions phosphorus appears to be the stronger predictor (i.e. Arvola et al. 2011). Furthermore in contrast to the results from modeling cyanobacterial biomass, we found that the strength of nitrogen and phosphorus as predictors of chlorophyll *a* were comparable. These results, combined with the path analysis, which shows that the effect of nitrogen is mediated through the production of all phytoplankton, suggests that the importance of nitrogen is particularly relevant when cyanobacteria become a dominant proportion of the autotrophs.

This interpretation is consistent with Dolman et al. (2012), who found that median cyanobacterial biovolume (i.e. biomass) increased in a linear fashion across a large TN gradient of North German lakes whereas the relationship with TP was sigmoidal with an inflection point at TP concentrations of ~50 μg L^{-1}. One explanation for this close association of cyanobacteria with TN is that cyanobacteria may have intrinsically higher N requirements than eukaryotic algae as a result of their important phycobiliprotein accessory pigments (Allen 1984). Cyanobacteria have some of the highest protein contents measured in microbes (Becker 1994). Alternatively the capacity for nitrogen fixation in some cyanobacteria might enable total nitrogen to rise concomitantly with cyanobacterial biomass. In this regard, Klausmeier et al. (2004) found that N_2-fixing cyanobacteria tend to have higher cellular N:P ratios than non-fixing phytoplankton. Nitrogen fixation arises when nitrogen is severely limiting which often occurs under high phosphorus loading. However, some studies have suggested that the capacity for nitrogen fixation is not always enough to

compensate for N limitation due to micro-element (Wurtsbaugh and Horne 1983) or light limitation (Lewis and Levine 1984).

To our knowledge, this is the first study to substantiate the influence of temperature on planktonic cyanobacterial biomass across a broad range of lake morphometries. The only comparable large-scale empirical modelling of cyanobacteria which considers temperature was done by Kosten et al. (2012) who focused on shallow European and South American lakes (i.e. defined as lakes less than 6 m). When the NLA dataset were separated into shallow (n=570) and deep lakes (n=575), we found that model variable selection in shallow lakes was comparable to that of the complete set, but that variance explained was actually lower than that found for deep lakes. This weaker predictive power might be reflective of the regime shift dynamics characteristic of shallow lakes (Scheffer 2005). With the deep lake dataset, again variable selection was consistent with the complete dataset, but the variance explained by surface temperature was greater (r^2_{adj}=0.17, p-value<0.05). The contrasting results between the deep and the shallow lake subsets suggest that lake water stratification may be part of the overall temperature signal.

Further separating these depth classes into natural lakes or reservoirs also highlighted distinctions (Fig 5; table 3), which are likely related to hydrological differences. Reservoirs are known to have shorter water residence times relative to lakes and are subject to larger water-level fluctuations (Kalff 2002). Cyanobacteria are sensitive to water residence times (Chetelat et al. 2006; Carvalho et al. 2011). Given this background, it was not surprising to find that the

strongest models were associated with the natural deep lakes, where nitrogen explained 32% of the variability in cyanobacterial biomass and temperature explained a small proportion of additional variation in the multivariate model (r^2_{adj}=0.33). Interestingly, in the natural subsets, additional predictors of cyanobacteria were identified: pH served as the best single predictor for shallow lakes and conductivity (which is correlated with pH, r=0.57) was the second best predictor for deep lakes (Fig. 5; Table 3). These results are consistent with previous, albeit smaller scale studies, that demonstrated an association between cyanobacteria and high pH (Brock 1973) or alkalinity (Carvalho et al. 2011), as well as high salinity (Tonk et al. 2007).

The multiple linear regression analyses show that even once the effect of nutrients is accounted for, cyanobacterial biomass increases as a positive function of temperature between 10 and 37ºC (Table 2). Path analysis provides further insight suggesting that water temperature has a direct effect on cyanobacterial biomass. These inferences are consistent with experimental data, which suggest that maximal growth rates occur at higher temperatures in cyanobacteria than in eukaryotic phytoplankton (Robarts & Zohary, 1987, Paerl et al. 2011, but see Carey et al. 2012). Furthermore, cyanobacteria can outcompete other algal groups under variable nutrient conditions at temperatures greater than 24°C in chemostat experiments with natural assemblages (Tilman et al. 1986). Analyses from whole-lake experimental manipulations (Jöhnk et al. 2008) and long-term data sets (e.g. Wagner and Adrian 2009) have also shown that water column stability (which is related to temperature) is an additional trigger of cyanobacterial blooms.

Considering the projections of global warming (Meehl et al. 2007), efforts to reduce nutrient loading to lakes may not result in decreases in cyanobacteria (Posch et al. 2012). It has been estimated that under scenarios of atmospheric CO_2 doubling from 1990 levels, maximum lake surface water temperature can be expected to rise on average 3.3ºC in the United States (Fang and Stefan 2009). Applying this water temperature increase to the median surface lake water temperature of NLA lakes under median TN concentrations, we would predict, based on our multivariate TN-surface temperature model (assuming that nutrients and light are sufficient to support this growth), a doubling of cyanobacterial biomass (from 238 μg L^{-1} to 510 μg L^{-1}). In contrast, chlorophyll *a* concentrations would be expected to increase only by 36% (from 8.64 μg L^{-1} to 11.72 μg L^{-1}) under the same conditions.

The models described herein cover a wide range in nutrients and temperature variables, but the variance explained is modest. These results, however, are not surprising given that the data are based on single lake samples. Using a similar snapshot approach, Kosten et al (2011) reported coefficients of determination for shallow lakes (n=143) that are comparable to the ones reported here. In contrast, studies where cyanobacterial data were collected and averaged across the growing season tend to produce stronger models (Trimbee and Prepas, 1987; Downing et al. 2001). Håkanson's (2007) analysis suggests that cyanobacteria are among the most temporally-dynamic lake constituents. As such, the predictive models presented here would likely be improved through multiple sampling.

Collectively, this analysis of the ~ 1000 lake NLA dataset provides strong evidence that increases in nitrogen and temperature, in addition to phosphorus, are associated with increases in cyanobacterial biomass. If society continues along the trajectory charted during the last century (Tilman et al. 2001; Meehl et al. 2007; Holtgrieve et al. 2011), cyanobacterial biomass and hence cyanobacterial blooms will become more expansive and frequent. Given that many lakes and reservoirs represent sources of drinking water and hotspots for biodiversity (Strayer and Dudgeon, 2010), these results are of considerable concern. With ~30% of US lakes already falling within risk categories of the WHO guidelines for cyanotoxins, it is critical to mitigate nutrient and climate change stressors.

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Tables

Table 1: Distribution of variables across the United States National Lakes Assessment data set (n=1147, USEPA 2009). Biomass was estimated from the original cell density data and functional grouping is based on the cyanobacterial taxonomic literature (see methods for details).

variables	min	max	mean	median
Area (ha)	4	167490	1237	70
Secchi depth (m)	0.04	36.71	2	1.38
Max depth (m)	<1	97	10	6
Conductivity ($\mu s\ cm^{-1}$)	4	50590	665	242
pH	4.1	10.3	8.1	8.2
Surface Temperature (°C)	10	38	24	25
Mean Temperature (°C)	7	34	21	21
Chlorophyll-a ($\mu g\ L^{-1}$)	<1	936	28	8
Total Nitrogen ($\mu g\ L^{-1}$)	5	26100	1167	568
Total Phosphorus ($\mu g\ L^{-1}$)	<1	4679	107	24
Cyanobacteria cell density (10^6 cells L^{-1})	0	4980	34.3	5.05
Cyanobacterial biomass ($\mu g\ L^{-1}$)	0	200257	2148	349
Bloom-forming cyanobacterial biomass ($\mu g\ L^{-1}$)	0	200257	1512	182
Potentially toxic cyanobacteria biomass ($\mu g\ L^{-1}$)	0	200257	1906	274
Heterocystous cyanobacteria biomass ($\mu g\ L^{-1}$)	0	74885	577	7
Potentially fixing cyanobacteria biomass ($\mu g\ L^{-1}$)	0	74885	1153	62

Table 2: Predictive linear models for chlorophyll *a*, cyanobacterial biomass and various cyanobacterial functional groups based on NLA data (USEPA 2009), with only the best fitting multivariate model reported. Predictors include chlorophyll a (chl *a*); total nitrogen (TN); total phosphorus (TP); mean water-column temperature (MWT); surface water-column temperature (SWT); conductivity (Cond ; µS). All concentrations in μg L^{-1} and temperatures in °C.

Linear model	r^2_{adj}	BIC	F	*df*
Chlorophyll *a* (*n*=1142)				
Log10 Chl *a* = -1.96 + 1.04 log10 TN	0.53	1460	1296	1141
Log10 Chl *a* = -0.03 + 0.66 log10 TP	0.52	1492	1229	1141
Log10 Chl *a* = -0.46 + 0.06 MWT	0.27	1966	424	1141
Log10 Chl *a* = -0.38 + 0.05 SWT	0.11	2188	148.6	1141
Log10 Chl *a* = -2.79 + 0.99 log10 TN + 0.04 SWT	0.59	1309	827.9	1140
cyanobacterial biomass (*n*=1148)				
Log10 CBB = 1.24 + 1.11 log10 Chl *a*	0.28	3674	435.9	1147
Log10 CBB = -1.14 + 1.22 log10 TN	0.17	3850	228	1147
Log10 CBB = 0.19 + 0.10 MWT	0.13	3891	180.3	1147
Log10 CBB =1.28 + 0.69 log10 TP	0.12	3905	163.3	1147
Log10 CBB = -0.48 + 0.11 SWT	0.11	3920	146.8	1147
Log10 CBB = -3.18 + 1.11 log10 TN + 0.10 SWT	0.25	3739	188.5	1146
Bloom-forming cyanobacterial biomass (*n*=975)				
Log10 BCBB = 1.48 + 0.92 log10 Chl *a*	0.34	2401	492.4	974
Log10 BCBB = 1.43 + 0.65 log10 TP	0.19	2603	231.1	974
Log10 BCBB = -0.47 + 1.02 log10 TN	0.19	2609	223.9	974
Log10 BCBB = 1.00 + 0.06 MWT	0.1	2713	103.5	974
Log10 BCBB = 0.92 + 0.06 SWT	0.05	2761	51.8	974
Log10 BCBB = -1.59 + 0.98 log10 TN + 0.05 SWT	0.22	2573	138.5	973
Potentially toxigenic cyanobacterial biomass (*n*=1052)				
Log10 TCBB = 1.44 + 1.00 log10 Chl *a*	0.35	2718	566.5	1051
Log10 TCBB = -0.66 + 1.09 log10 TN	0.2	2953	259.4	1051
Log10 TCBB = 1.45 + 0.65 log10 TP	0.18	2981	224.4	1051
Log10 TCBB = 0.77 + 0.08 log10 MWT	0.12	3045	149.1	1051
Log10 TCBB = 0.24 + 0.75 log10 Cond	0.11	3012	125.2	1051
Log10 TCBB = -2.14 + 1.04 log10 TN + 0.07 SWT	0.25	2881	180.7	1050
Heterocyst-producing cyanobacterial biomass (*n*=755)				
Log10 HCBB = 0.65 + 1.00 log10 Chl *a*	0.29	2131	310.5	754
Log10 HCBB = -2.19 + 1.38 log10 TN	0.24	2192	240.6	754
Log10 HCBB = 0.47 + 0.82 log10 TP	0.22	2216	208.7	754
Log10 TCBB = -3.06 + 0.58 pH	0.17	2257	150.7	754
Log10 TCBB = -0.14 + 0.78 log10 Cond	0.12	2306	101.3	754
Log10 TCBB = -4.35 + 1.10 log10 TN + 0.36 pH	0.29	2137	157.8	753

Table 3: Predictive models of cyanobacterial biomass (CBB) based on lake type, with only the best fitting multivariate model reported. Predictors include total nitrogen (TN) ; total phosphorus (TP); pH; surface water-column temperature (SWT); mean water-column temperature (MWT); and conductivity (Cond ; ìS). All concentrations were measured in *ì*gL^{-1}and temperatures in °C.

subset	linear model	r^2_{adj}	BIC	AIC	*df*
Natural lakes	-1.67 + 1.38 log10 TN	0.25	1756	1743	516
	1.14 + 0.82 log10 TP	0.19	1795	1782	516
	-2.88 + 0.63 pH	0.17	1805	1793	516
	-3.29 + 1.26 log10 TN + 0.09 SWT	0.3	1726	1709	515
Reservoirs	-0.24 + 0.11 MWT	0.16	2048	2035	629
	-0.68 + 0.12 SWT	0.13	2069	2056	629
	-0.52 + 1.03 log10 TN	0.09	2101	2088	629
	-2.84 + 0.88 log10 TN + 0.11 SWT	0.2	2027	2009	628
Deep lakes	-1.99 + 1.56 log10 TN	0.18	1948	1935	559
	-1.30 + 0.14 SWT	0.17	1952	1938	559
	0.06 + 0.10 MWT	0.15	1968	1955	559
	-3.41 + 1.16 log10 TN + 0.10 SWT	0.26	1893	1875	558
Shallow lakes	-0.35 + 0.96 log10 TN	0.1	1908	1895	584
	1.57 + 0.55 log10 TP	0.07	1927	1914	584
	0.61 + 0.08 MWT	0.05	1937	1924	584
	-2.96 + 1.09 log10 TN + 0.09 SWT	0.17	1867	1850	583
Deep natural lakes	-3.26 + 2.05 log10 TN	0.32	829	819	243
	-0.71 + 1.24 log10 Cond	0.23	861	850	243
	0.97 + 1.06 log10 TP	0.17	879	869	243
	-7.50 + 1.79 log10 TN + 5.45 pH	0.34	801	788	242
	-3.90 + 1.79 log10 TN + 0.06 SWT	0.33	828	814	242
Deep reservoirs	-0.55 + 0.13 MWT	0.21	1070	1059	315
	-1.44 + 0.14 SWT	0.19	1077	1066	315
	-0.74 + 1.09 log10 TN	0.08	1118	1107	315
	-1.82 + 0.50 log TP + 0.13 SWT	0.24	1046	1031	314
	-3.01 + 0.74 log10 TN + 0.13 SWT	0.23	1068	1052	314
Shallow natural lakes	-1.78 + 0.53 pH	0.15	922	911	262
	-1.08 + 1.17 log10 TN	0.15	922	912	262
	1.19 + 0.76 log10 TP	0.14	926	915	262
	-3.64 + 1.26 log10 TN + 0.10 SWT	0.21	906	892	261
Shallow reservoirs	0.50 + 0.08 MWT	0.06	988	976	306
	0.53 + 0.08 SWT	0.06	988	977	306
	0.21 + 0.80 log10 TN	0.05	990	979	306
	-2.09 + 0.86 log10 TN + 0.08 SWT	0.12	973	958	305

Figures

Figure 1. Regression of estimated cyanobacterial biomass (derived from literature values) against measured cyanobacterial biomass (based on microscopic measurements of cells and colonies). The data are from lakes distributed across three Canadian provinces: 1) Alberta (AB; n=10); 2) British Columbia (BC; n=24); and, 3) Ontario (ON; n=26). The black line represents the best fit linear regression (log10 estimated CBB = -0.1 + 1.1 log10 measured CBB, r^2_{adj}=0.90, p-value< 0.001) and the 1:1 line is shown in grey.

Figure 2. Distribution of nutrient, temperature and phycological variables across NLA sites. A) Total nitrogen (TN); B) Total phosphorus (TP); C) Surface water temperature (Surf T); D) Elevation (Elev); E) chlorophyll a (Chl-*a*); F) log Cyanobacterial biomass (log CBB). Total nitrogen, total phosphorus and chlorophyll a are binned by lake trophic status (Kalff 2002).

Figure 3. Correlation matrix of the predictors of cyanobacterial biomass. Left panels report linear correlation coefficients, right panel shows the relationship with a LOESS smoother, diagonal shows distribution of the variables: log chlorophyll a, log total nitrogen, log total phosphorus, log maximum lake depth, surface water temperature (surface T) and mean water-column temperature (mean T).

Figure 4. Univariate linear regression models. Cyanobacterial biomass as predicted by A) log chlorophyll *a*, B) log total nitrogen, C) mean water column temperature and D) log total phosphorus. Natural lakes (n=516) are shown in grey and reservoirs (n=629) in black. Table 2 and 3 include model equations and goodness-of-fit. Detection limits indicated by the grey dashed lines.

Figure 5. Alternative path analysis scenarios predicting cyanobacterial biomass using the main variables selected through linear regression. A) Total nitrogen and surface temperature are indirect effects and total phytoplankton biomass (chlorophyll *a*) is a direct effect on cyanobacterial biomass, B) idem to model described in (A) but with nutrients also acting directly on cyanobacterial biomass, C) idem to model described in (A) but with surface temperature also acting directly on cyanobacterial biomass. Chi-square, goodness-of-fit index (GOF) and Bayesian Information Criterion (BIC) values for each model are reported.

Figure 6. Strongest predictors of cyanobacterial biomass and associated regression coefficients when dataset separated by lake depth (<6m ; >6m) and origin (natural lakes ;reservoirs). The variables considered were total nitrogen (TN), total phosphorus (TP), mean water-column temperature (MWT), surface water temperature (SWT), pH and conductivity (Cond).

Figure 1

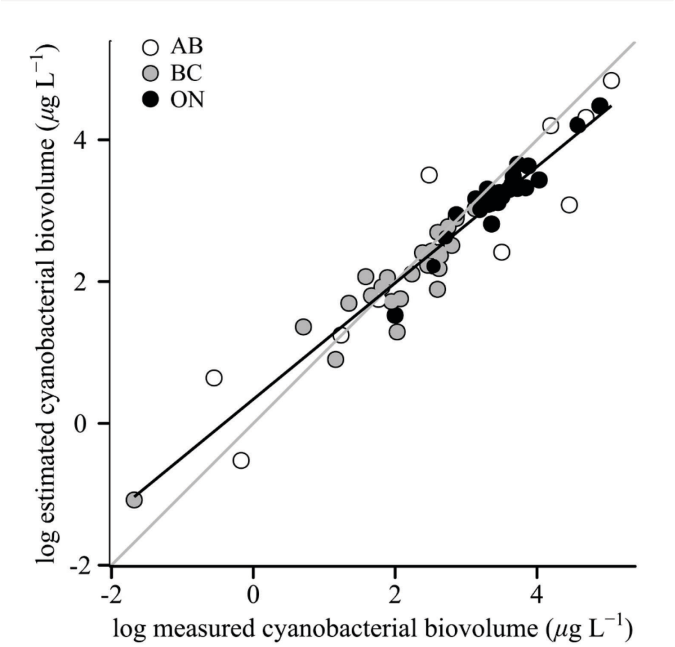

AB
BC
ON
log estimated cyanobacterial biovolume (μg L^{-1})
log measured cyanobacterial biovolume (μg L^{-1})
-2
0
2
4

Figure 2

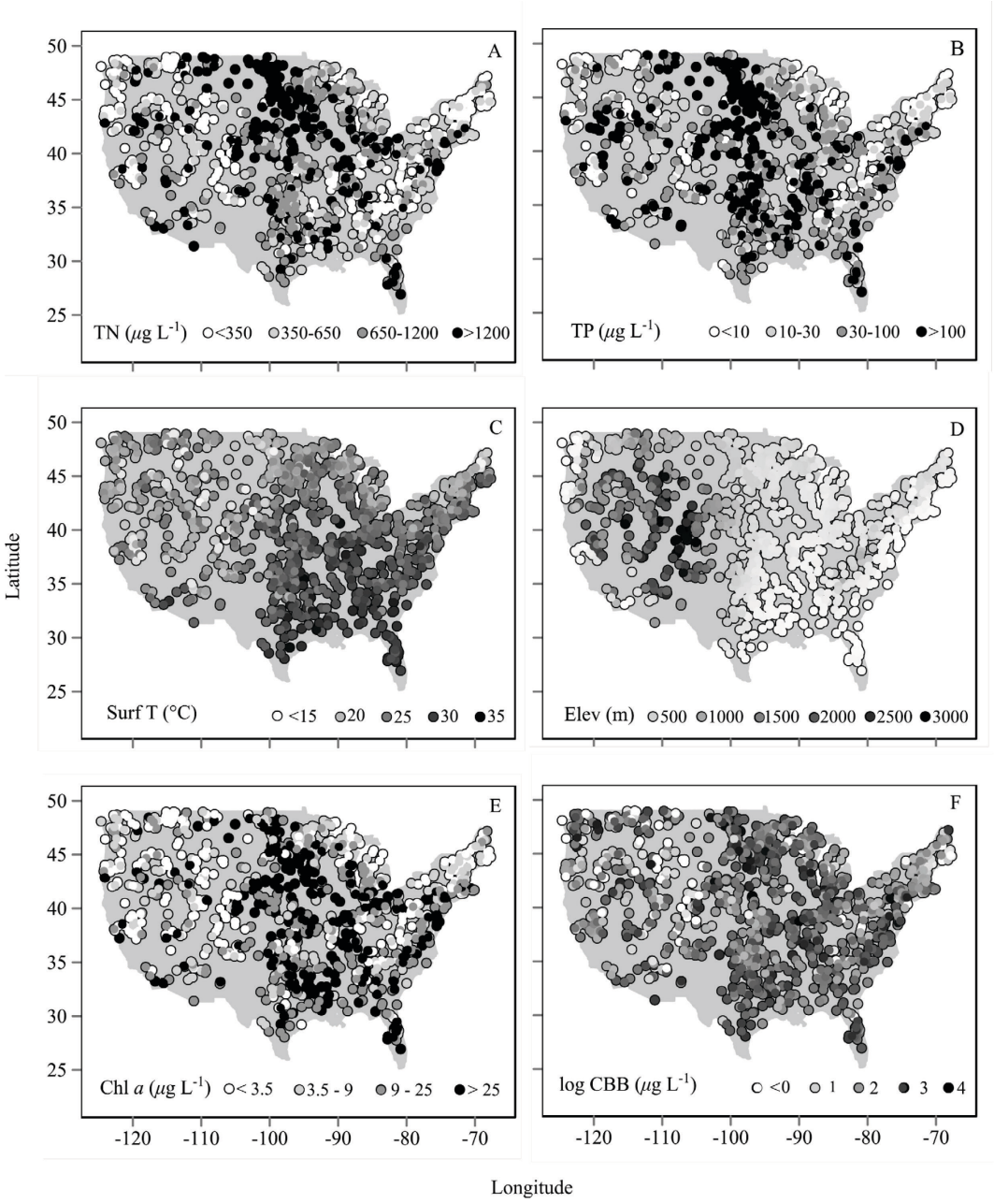

A
TN (μg L-1) ○<350 ○350-650 ●650-1200 ●>1200
B
TP (μg L-1) ○<10 ○10-30 ●30-100 ●>100
C
Surf T (°C) ○ <15 ○20 ●25 ●30 ●35
D
Elev (m) ○500 ○1000 ●1500 ●2000 ●2500 ●3000
E
Chl a (μg L-1) ○< 3.5 ○3.5 - 9 ●9 - 25 ●> 25
F
log CBB (μg L-1) ○ <0 ○ 1 ● 2 ● 3 ● 4
50
45
40
35
30
25
-120
-110
-100
-90
-80
-70
Latitude
Longitude

Figure 3

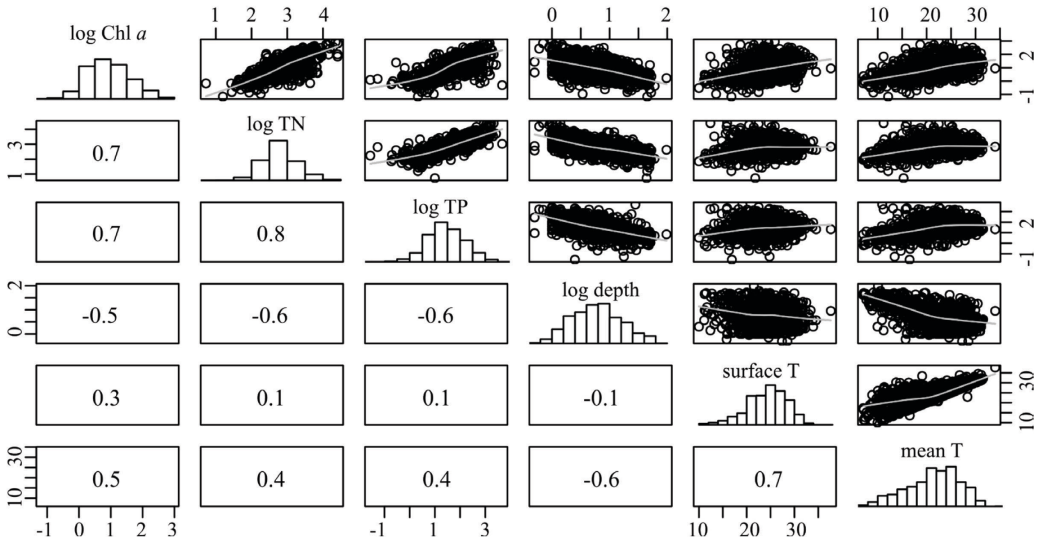

log Chl a
log TN
log TP
log depth
surface T
mean T
0.7
0.7
0.8
-0.5
-0.6
-0.6
0.3
0.1
0.1
-0.1
0.5
0.4
0.4
-0.6
0.7

Figure 4

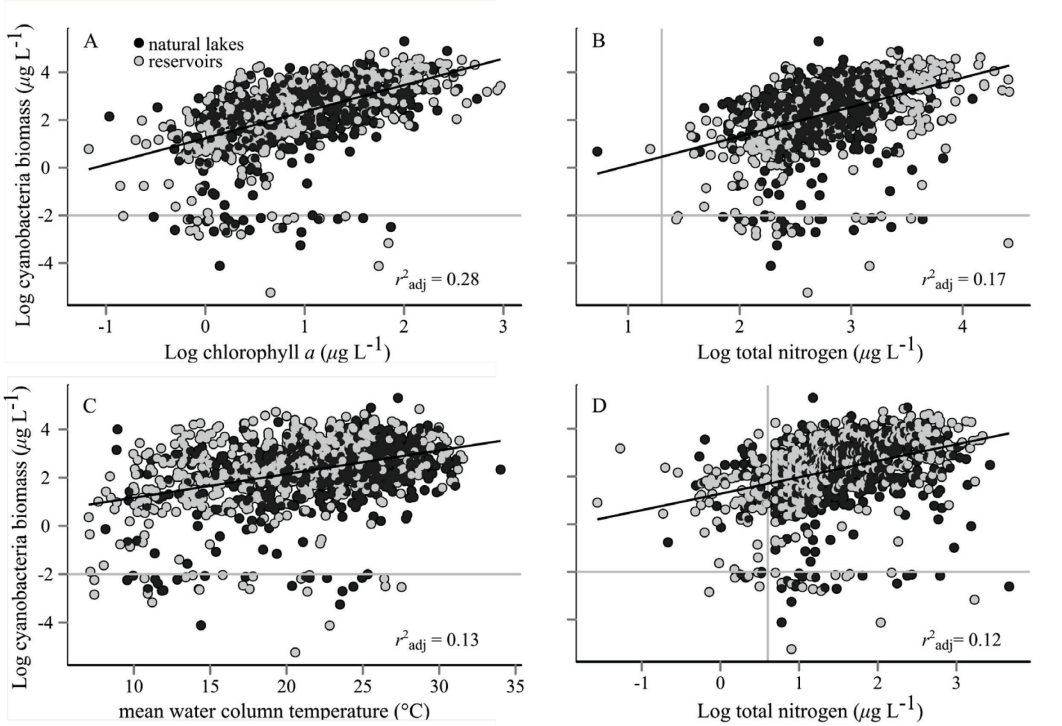

A
natural lakes
reservoirs
Log cyanobacteria biomass (μg L-1)
Log chlorophyll a (μg L-1)
r2adj = 0.28
B
Log total nitrogen (μg L-1)
r2adj = 0.17
C
mean water column temperature (°C)
r2adj = 0.13
D
Log total nitrogen (μg L-1)
r2adj= 0.12

Figure 5

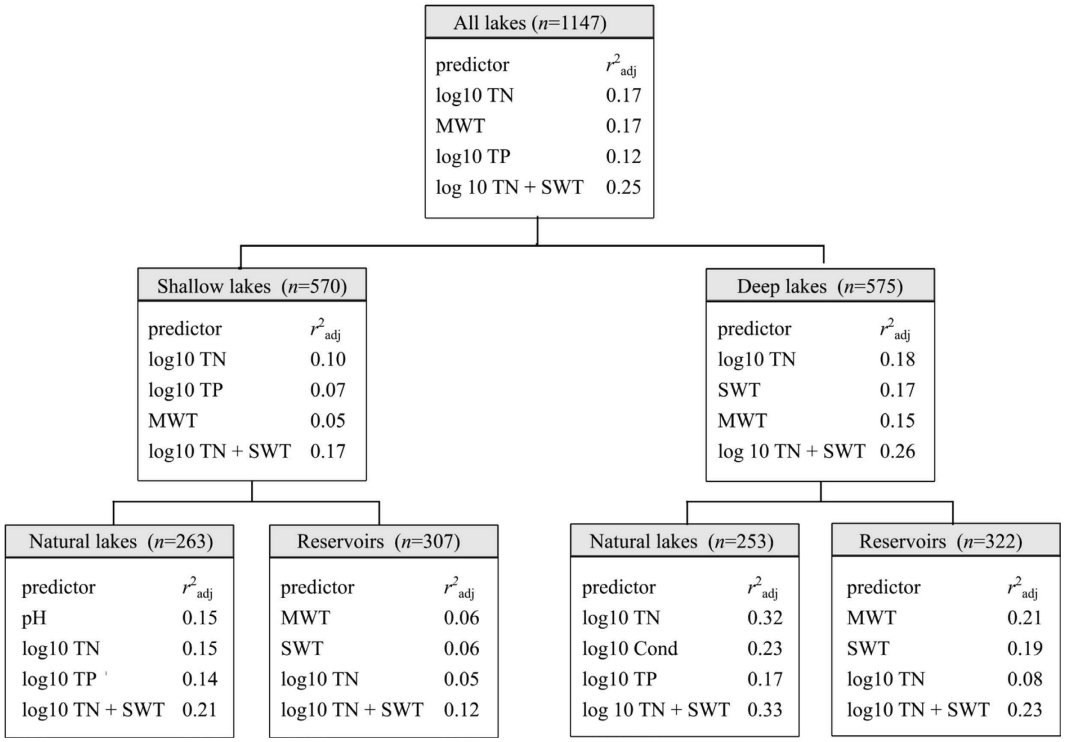
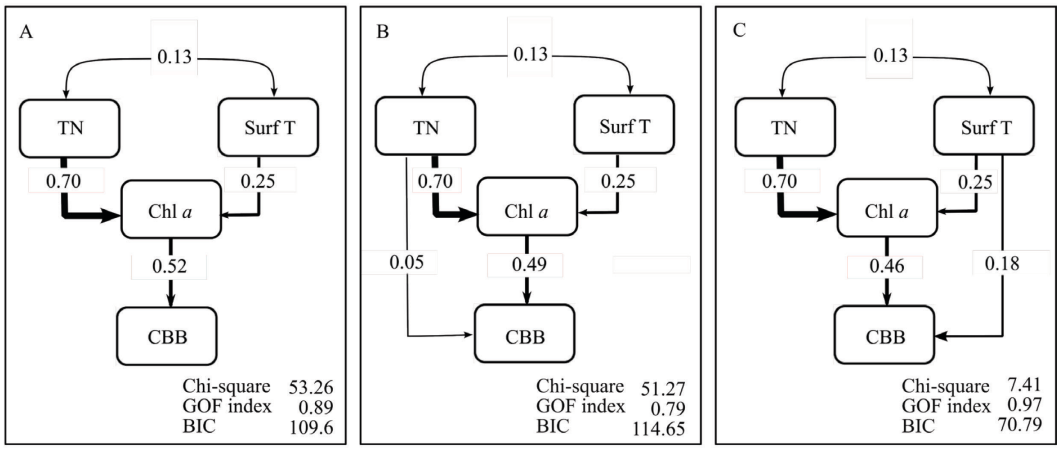

All lakes (n=1147)
predictor r^2_{adj}
log10 TN 0.17
MWT 0.17
log10 TP 0.12
log 10 TN + SWT 0.25
Shallow lakes (n=570)
predictor r^2_{adj}
log10 TN 0.10
log10 TP 0.07
MWT 0.05
log10 TN + SWT 0.17
Deep lakes (n=575)
predictor r^2_{adj}
log10 TN 0.18
SWT 0.17
MWT 0.15
log 10 TN + SWT 0.26
Natural lakes (n=263)
predictor r^2_{adj}
pH 0.15
log10 TN 0.15
log10 TP 0.14
log10 TN + SWT 0.21
Reservoirs (n=307)
predictor r^2_{adj}
MWT 0.06
SWT 0.06
log10 TN 0.05
log10 TN + SWT 0.12
Natural lakes (n=253)
predictor r^2_{adj}
log10 TN 0.32
log10 Cond 0.23
log10 TP 0.17
log 10 TN + SWT 0.33
Reservoirs (n=322)
predictor r^2_{adj}
MWT 0.21
SWT 0.19
log10 TN 0.08
log10 TN + SWT 0.23

Figure 6


A
0.13
TN
Surf T
0.70
0.25
Chl a
0.52
CBB
Chi-square 53.26
GOF index 0.89
BIC 109.6
B
0.13
TN
Surf T
0.70
0.25
Chl a
0.05
0.49
CBB
Chi-square 51.27
GOF index 0.79
BIC 114.65
C
0.13
TN
Surf T
0.70
0.25
Chl a
0.46
0.18
CBB
Chi-square 7.41
GOF index 0.97
BIC 70.79

Connecting Statement

In the first chapter I took advantage of a very large-scale dataset spanning large nutrient and temperature gradients to develop predictive cyanobacterial models. This analysis showed that nutrients and temperature explained a significant amount of the variation in cyanobacterial biomass in US lakes. I also found that part of the temperature effect on cyanobacteria can be partitioned uniquely from that which all phytoplankton experience (as expressed by chlorophyll a concentrations). This result supports the findings of lab experiments and what has been reported anecdotally, that increasing temperatures favour cyanobacterial species. Furthermore, I found that strength and characteristics of the models developed varied across basin type.

The strength of this analysis is that it covers a large number of lakes spanning a substantial geographic extent that were sampled using consistent methods. However, the variance in cyanobacterial biomass explained by our models is modest, but comparable to other models based on snapshot samples. Therefore, in chapter two I have therefore focused my analysis on Canadian lakes, for which we obtained data spanning multiple dates over the growing season. In this chapter, I also applied a mixed-modelling framework to answer the question: how different are predictive cyanobacterial biomass models across regions?

Predictive cyanobacterial biomass and community models from Canada

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Keywords: cyanobacteria, nitrogen, phosphorus, temperature, climate, Canadian lakes, regional models

Running title: Cyanobacterial biomass in Canada.

Target Journal: Canadian Journal of Fisheries and Aquatic Sciences

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Abstract

Increased cyanobacterial bloom reporting around the world has prompted the need for a closer evaluation of empirical models. Using seasonally integrated data from 88 lakes spread across Alberta, British Columbia and Ontario, we modelled cyanobacterial biomass as a function of nutrients, water chemistry, temperature and water column-stability. We found nutrients were the best predictors using a general linear modelling approach, with total Kjeldahl nitrogen explaining significantly more variance in cyanobacterial biomass (54%) than total nitrogen and total phosphorus. Effects of temperature-dependent variables, though significant, were confounded by their high colinearity with nutrient concentrations. Mixed-effects models improved significantly the fit of the general linear models by varying slopes and intercepts for the predictors among regions. We attribute these random effects to the strong environmental differences between Ontario and the western provinces, although the differences in ranges in multiple variables between the two subsets preclude us from concluding that these trends would hold up with a larger dataset. To our knowledge, this study is the first attempt to model cyanobacterial abundances across Canada. The inclusion of a greater number of lakes, especially nutrient-rich Ontario lakes would allow us to further refine this Canadian model.

Cyanobacterial blooms are a concern worldwide because they form unsightly oxygen-depleting scums and their toxins negatively impact the use of water bodies for drinking water and recreation. A growing public concern may account for the increased reporting of blooms over the past decade (Winter et al. 2011), but numerous review papers have also suggested that conditions favourable for bloom-events have increased in recent years (Paerl and Huisman 2009). It is generally understood that cyanobacterial biomass and dominance increase with rising concentrations of total nutrients (e.g Pick and Lean 1987; Downing et al. 2001). However, other factors that can also be important drivers of cyanobacteria are water temperature and water-column stability (e.g. Kosten et al. 2012; Taranu et al. 2012).

Previous empirical cyanobacterial models have been either constructed across large spatial gradients or for localized areas (see Table 1), but there has been only been a limited amount of work examining how cyanobacterial models vary across regions. To our knowledge the only example of such comparative work was done by Trimbee and Prepas (1987) who tested general nutrient models developed by Smith (1983). Trimbee and Prepas (1987) found that the published models consistently underestimated cyanobacterial dominance in Alberta. Additionally they found that TP was a better predictor of cyanobacterial dominance than TN or the N:P ratio found by Smith (1983). Differences in geology, hydrology and pedology, in addition to human activities, can affect the ranges of nutrients as well as other key variables such as dissolved organic carbon, pH and light among regions. Such differences combined with climatic-

induced signals may result in differential responses to the parameters driving cyanobacterial abundance and dominance. Though cyanobacteria are generally thought of as cosmopolitan, differences in cyanobacterial communities among regions may be another reason for discrepancies in response models among regions.

Over the past two decades, our understanding of the parameters that can influence cyanobacteria abundances has greatly improved, but it remains difficult to ascertain the risks associated with particular water bodies and the relative effects of nutrients and temperature in driving the observed changes. Using datasets provided by the Ministry of Environment from several provinces across Canada (Alberta, British Columbia, Ontario), we constructed models to assess the relative importance of temperature, water-column stability, and nutrients in driving cyanobacterial biomass and dominance. We adopted a mixed-effect modelling approach to account for regional differences in modulating the response of cyanobacteria to environmental parameters. Given that an estimated 75% of the population in Canada relies on surface water as drinking water (Statistics Canada, 2010), the goal of this research is to enhance the ability to predict bloom events and identify high risk regions over a large territory.

Methods

Phycological, chemical and physical data were provided to us by the Ministries of the Environment of Alberta (AB), British-Columbia (BC), and Ontario (ON). There were notable regional differences across these provinces; Alberta lakes in this dataset are naturally meso-eutrophic to hypereutrophic

because of the underlying sedimentary bedrock as well as agricultural activities (Taranu et al., 2009). In contrast, study lakes from Ontario were oligo-mesotrophic and principally located on the Canadian Shield. Our study lakes from British Columbia are of intermediate trophic status. The broad geographic distribution of our study sites also provides a large range in climates from continental Interior British Columbia to the Prairie Parklands of Alberta and the North Eastern Forests of Ontario.

Given that the data came from three different sources, a number of steps were taken to create a comparable dataset. For example, much of the Ontario phycological data consisted of seasonal composite samples. In these samples, integrated water samples from the euphotic zone are collected throughout the growing season and combined before sample processing to yield a growing-season average concentration of algae. To create comparable data for lakes in Alberta and British Columbia, phycological samples from sampling dates across the growing season (estimated for all lakes as ranging from May to October) were averaged. Alberta data was most comparable to Ontario data as samples were also depth integrated over the euphotic zone (~2x secchi depth) and algal biovolumes were reported. Phycological data from British Columbia was based uniquely on cell counts and consisted mainly of surface grabs. To convert cell counts into biomass, we applied a calibration model based on cell volume averages from the literature (described in Beaulieu et al. chap. 1). For lakes with data spanning several years, a single year was haphazardly selected.

Lake chemistry results were generally based on analyses of euphotic zone samples, where multiple depths were averaged. Variables of interest were total

nutrients (total phosphorus (TP), total nitrogen (TN)), nitrogen species (nitrite-nitrate, ammonia-ammonium, total Kjeldahl nitrogen) and other factors that have been shown to influence cyanobacteria abundances (N:P ratio, pH, conductivity). All variables were averaged over the growing-season.

Temperature profile data were used to construct the following variables: average surface water temperature, average depth-integrated water temperature, and average August surface water temperate as this was the month with the highest surface water and generally corresponds to the time where cyanobacteria may achieve dominance in temperate lakes (pers. obs.). The strength of stratification at the thermocline was calculated using the Brunt-Väisälä buoyancy frequency (N, s^{-1}). Briefly, we identified the depth of maximal temperature change for each temperature profile and then estimated the density gradient between 0.5m above and below this depth in relation to the entire water column (following the equations provided in Jennings et al. 2012). The average N (amN; average thermocline stability) and max N (mmN; maximal stratification encountered over the growing season) were then computed.

Using the main variables of interest (TP, TN, TN species, surface temperature, depth integrated water temperature August surface temperature, amN, mmN)) we first applied general univariate linear models (GLMs) to predict cyanobacterial biomass. We then constructed mixed-effects models from the general models developed to introduce province as random effects. Model selection of these nested designs was tested through ANOVA. The significance of the selected fixed variables was re-tested after the introduction of the random effects. This model structure assumes that while the data in general can be fitted

to a general model, unexplained variance in each province can be further reduced by allowing some of the residual variance to be modelled differently by region.

To explore whether cyanobacteria community composition was different at the regional scale, we conducted ordination analyses of cyanobacterial genera across Alberta lakes. Data from British Columbia contained too few sites and the consistently low cyanobacterial biomasses in Ontario samples made these two regions unsuitable for this type of analysis. Detrended correspondance analysis informed the decision to perform constrained ordination using Canonical Correspondance Analysis (CCA). For each of the environmental variables considered for linear regression, we performed a single-variable CCA. Variables were then ordered based on their significance as community predictors and for highly correlated variables ($r > 0.5$), we conserved uniquely the best predictor. These variables were introduced into a model and, through backwards selection, variables that did not contribute to the model were removed.

Results

Significant differences in cyanobacterial biomass were found across provinces. Cyanobacteria were most abundant in Alberta lakes, where biomasses were up to two orders of magnitude greater than in Ontario lakes (Fig. 1). Cyanobacterial dominance followed a similar trend, though the range was much greater in Alberta lakes than in the other provinces. Significant differences were found for numerous environmental predictors including surface water temperature, August surface water temperature (month with maximum surface water temperature), average thermocline stability (amN), total nitrogen, total

phosphorus, conductivity and pH (Fig. 1)

In terms of community composition, cyanobacteria were the dominant group in Alberta lakes whereas Ontario lakes were dominated by chlorophytes. However, in terms of absolute biomass, the contribution of chlorophytes was similar between both provinces (Fig. 2). Considering only the cyanobacteria, we found the Nostocales *Anabaena* and *Aphanizomenon* genera to be the most abundant across all regions accounting for over 70% of the cyanobacterial biomass. *Oscillatoria (*previously known as *Planktothrix)* was a dominant genus in BC and AB. Taxa present in modest relative abundances in a single province were: 1) the colonial *Aphanothece* and *Chroococcus* in Ontario lakes; 2) *Microcystis* in Alberta; and, 3) *Lyngbya*, a benthic cyanobacteria, in BC (Fig. 2).

Considering the entire dataset, we found nutrient concentrations to be strong predictors of cyanobacterial abundance (Table 2; Fig. 3). We found that total Kjeldahl nitrogen was a significantly better predictor of cyanobacterial biomass than total phosphorus or total nitrogen. Seasonally-averaged water-column stability was the best temperature-related driver, with the best fitting linear model explaining 46% of the variance. August surface water temperature and average surface water temperature explained slightly less variance (r^2 adj = 0.39; 0.35). Interestingly pH was found to be the best single predictor of cyanobacterial biomass across all provinces, explaining 56% of the variability. However, the relatively high AIC of the pH model, together with the presence of distinct clusters in the pH distribution, demonstrates that this model is not the most statistically robust. Given that many of the environmental variables were collinear within the pan-Canadian dataset, we chose not to pursue multivariate

models (Fig. 4).

We used mixed-effect linear modelling (LMm) to refine the general univariate models to test for regional effects (Fig. 5). For TP and TN, the random intercept and random slope models yielded stronger results than the GLM models based on AIC (TP: 217<227 ; TN: 217 <225). For the other variables, the random intercept models generally provided the best fit and again these models consistently outperformed the linear models. pH was the only predictor for which the GLM was selected as the best model through nested ANOVA structure. However, for most environmental variables, we failed to develop a significant common model structure (aka fixed effect) in the mixed effects modelling framework as the variance was mostly explained by regional trends (random effects). Strong regional differences are apparent between the Ontario vs. Alberta and BC datasets (Fig. 1) and when we applied GLMs to the Ontario dataset alone, we found that models were weak and that the only significant explanatory variables were with pH and conductivity ($r^2_{adj} = 0.05$; $r^2_{adj} = 0.11$; $p < 0.05$ in both cases). When we only used data from Alberta and British Columbia, we found that the mixed-effect models explained a similar proportion of the variance compared than the linear models. Specifically, we found that the best univariate GLM explains up to 62% of the variance in cyanobacterial biomass with the best predictor (log TP) whereas the mixed-effect model explained the same amount of variance (using an estimate derived from the pseudo r^2) For this subset of the data pH and conductivity were poor predictors as were the temperature-related variables (although a number of the latter predictors were significant).

Consistent with the linear modelling work, nutrient and temperature-

related variables were also significant predictors of community composition in Alberta (Fig. 6; note: in this region nutrients and temperature-related variables were not significantly colinear). We found that 40% of the variance in cyanobacterial composition in Alberta lakes was explained by the first two axes of our canonical correspondance analysis. The first and second component axis explained respectively 25% and 15% of the variance. Of the nutrient variables selected, total phosphorus is a major contributor to the first axis whereas ammonia and nitrate-nitrite contributed mainly to the second axis. Average thermocline stability and August surface temperature contributed to both axes. We found that genera from the same class tended to be characterized by similar environmental conditions. For example, Oscillatoriales were associated with greater surface temperature and water column stability. The Synecchochocales species were associated with low stability and surface temperature and increased nitrate-nitrite. *Aphanizomenon* was associated with greater TP concentrations but *Anabaena*, the other N-fixing genera was not.

Discussion

The growing concern about increases in cyanobacterial abundances across globe has raised the question of how well predictive models developed from one region might apply to a different focal region. Furthermore, there has been very little evaluation of the relative merits of modelling of cyanobacterial abundances at regional vs continental scales. Despite discrepancies in sampling and processing methods across regions, we have developed robust models for cyanobacterial biomass. The advantage of a mixed-effect modelling approach is

that it allows one to appreciate how cyanobacterial responses to a particular environmental driver may vary across regions due to the effect of other environmental conditions (not included in the model), differences in range of environmental gradients or community differences.

Serious modelling efforts have been underway since the early 1980s following Smith's Science paper arguing that nutrient stoichiometry plays the strongest role in promoting cyanobacterial dominance. Since, models predicting cyanobacterial dominance and biomass have focused on nutrient concentrations as predictors (Table 1) as these large datasets offered little support to the N:P model. Consistent with these studies N:P is among the weakest models we developed, explaining 15% of the variance of cyanobacterial biomass.

Whereas temperature-related factors did serve to build statistically significant models, it is hard to isolate these effects from that of nutrients and other variables (Fig. 4). We know from experimental studies that cyanobacteria growth is enhanced by warmer temperatures (Robarts and Zohary 1987). However, we found the opposite relationship where cyanobacterial biomass across all regions was found to decrease with increasing water temperature. However, increasing water temperature was associated with a decrease in nutrients (our stronger predictor) and thus we think the temperature signal is simply to due its colinearity with nutrients. Lake survey studies where positive cyanobacteria-temperature effects have been detected (Kosten et al. 2012; Beaulieu et al. Chap 1) are based on much larger datasets where nutrients and temperature are not strongly collinear and that span extensive temperature gradients. For example, the range in mean temperature within our lakes is of

approximately 10 degrees Celsius whereas that reported within the North America Lake Assessment program was 27 degrees Celsius (for both surface and depth integrated temperature). That said, analyses of time series data have shown that even relatively small changes in temperature and stratification can be associated with significant increases in cyanobacteria abundances (Wagner and Adrian, 2009; Taranu et al. 2012); likely because of the limited variation in other environmental factors within single basin compared to the much larger changes across large lake surveys. Similar to the observation with surface water temperature, we found increased stratification to be related to lower cyanobacterial abundance, but the data were highly clustered (Fig. 4) and can be attributed to the distinct lake morphometries between regions.

With the mixed effect model, it was clear that there are strong regional differences in cyanobacterial response models. This is not surprising as there was little overlap in any of the environmental parameters between Ontario and western provinces: the Ontario lakes were generally more nutrient-poor and have longer growing seasons due to their more southerly latitude compared to the Alberta and BC lakes (Figure 1). Similarly, Prairie lakes tended to be naturally shallow and well-mixed whereas Ontario lakes were deep and stratified. Nonetheless, the models developed for BC and AB are consistent with one another and may be explained (at least in part) by the more similar environmental conditions between these regions (Figure 1).

It is well known that cyanobacteria are not a homogenous group and yet these data seem to be rarely considered (see Dolman et al 2012 as an exception). A particularly meaningful way to address questions related to community

composition is to focus on the specific traits (Litchman and Klausmeier, 2008; Table 3). For example, similar to previous studies (e.g. Hendzel et al. 1994 but see Dolman et al. 2012) we found some support for diazototrophs being associated with P-enriched systems (Fig. 5). Smaller colonial forms were found to be associated with colder well-mixed systems. Though little is known of the ecology of such species, they have been associated with intermittently flushed lakes (Mur et al. 1999). Based on this analysis, we would expect that with warming climate, stratified lakes in Alberta would experience an expansion of Nostacales cyanobacterial taxa (Sukenik et al. 2012). We would have like to also consider community differences among the different provinces, but this was not possible (see methods).

Overall, we believe that this is the first attempt to bring together a pan-Canadian analysis of cyanobacterial abundances in lakes. Even though slightly different sampling and counting methods have been used by the three agencies collecting the regional datasets, we found that our models are as strong as what has been reported in the literature (summarized in Table 1) and have comparable structures (Fig. 3). Our mixed-effects modelling framework improved the model fit in numerous cases, but was complicated by the lack of overlapping ranges for some variables. Concerted effort to sample productive lakes in Ontario could rectify this issue in the future. Certainly, this analysis is warranted as increased cyanobacterial bloom events under warming climatic conditions are a managerial concern across Canada. If we are to develop models that might allow us to foresee areas at risk, it is crucial to develop stronger databases on which to construct these models. This will require the collaboration of government,

research scientists and lake associations.

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Tables

Table 1: Previously developed predictive cyanobacterial models across spatial gradients

	Model type	Relationship found	R2	number of sites	sampling method	region
A Ecoregion/Continental scale						
Smith 1983		Dominance at TN:TP < 29 by weight	NA	17 lakes, multiple samples	seasonally integrated	North temperate (lakes)
Watson et al. 1997	quadratic	log CB (μgL^{-1}) = -0.613 + 2.97 log TP (μgL^{-1}) – 0.45 log TP^2	0.62	202 samples, 91 lakes	seasonally integrated	North temperate (lakes)
Downing et al. 2001	LM	ln(%CB/(100-%CB))= -10.0 + 3.03 log TN	0.42	204 ; 268	seasonally integrated	Temperate (lakes)
Kosten et al 2012	LM	log CB ($mm^3\ L^{-1}$) = -5.35 + 0.42 log TP ($ug\ L^{-1}$) + 0.01 Temp (°C) + 0.79 log TN (μgL^{-1})	0.28	143	snapshot	N Europe and S America (lakes)
Beaulieu et al (In review)	LM	log CB (μgL^{-1}) = -3.18 + 1.11 log TN (μgL^{-1}) + 0.1 Temp (°C)	0.25	1148	snapshot	United States
B Provincial/Regional scale						
Trimbee and Prepas 1987	LM	log CB (mgL^{-1}) = -1.92 + 1.34 log TP	0.67	36	seasonally integrated	Alberta + Smith data
Scheffer 1997		% Oscillatoria ~ Shade (+) , Secchi (-), Flush rates (-)	NA	118 samples, 55 lakes	seasonally integrated	Netherlands (shallow lakes)
Rolland et al. 2005	LM	log Microcystis ($\mu g\ C\ L^{-1}$) = 2.9 + 3 log kd -2.9 log TDN + 0.6 stratification log Anabaena ($\mu g\ C\ L^{-1}$) = -2.0 +2.8 log Kd -2.2 log TDP	0.71 ; 0.47	48 samples, 4 lakes	snapshot	Canada (Quebec) (eutrophic lakes)
Giani et al. 2005	LM	log CB (mg $C\ L^{-1}$)= -7.3 + 1.96 log TP (μgL^{-1})	0.64	22	snapshot	Canada (Quebec)
Hakanson et al. 2007	LM	$CB^{0.25}$ ($\mu g\ ww\ L^{-1}$)= 9.06 log TN -21.6	0.63	86	growing season median	Sweden (lakes), Denmark (lagoon)
Søndergaard et al. 2011	LM	%CB = 35.7 + 16.3 log TP ; %CB = 27.8 + 10.8 log TP + 13.9 log TN	0.09; 0.11	668 samples, 440 lakes	snapshot	Denmark (lakes)
Carvalho et al. 2011	GAMm	CB ~ Color (10-20 Pt L^{-1}), alkalinity (>1 mEq L^{-1}), retention time (>30 days), TP (>20 μgL^{-1})	NA	262 samples, 134 lakes	snapshot	UK (lakes)
Dolman et al. 2012		sigmoidal TP (flattening at 50 μgL^{-1}), continued TN	NA	102	late summer integrated	Northern Germany

Table 2: Linear and mixed-effects models developed for Canadian lakes. For the mixed-models we only report the best fitting type. Not shown is the mixed effects model for pH as the linear model provided the best fit.

		AIC	df	F	Adj. r^2
pH	-3.91*** + 0.80*** pH	214.01	85	110.9	0.56
TKN	-5.26*** + 2.71*** log TKN	209.29	80	96.37	0.54
TN	-5.42*** + 2.76*** log TN	224.83	86	92.62	0.51
TP	-0.22 + 1.88*** log TP	226.88	86	88.5	0.5
Average N	3.78*** - 32.71*** amN	233.16	86	76.49	0.46
Aug Surf T	8.87*** -0.33*** Aug Surf T	236.03	82	54.46	0.39
Conductivity	1.24*** + 0.0038*** Cond	241.72	83	50.55	0.37
Mean Surf T	7.04*** -0.30*** Surf T	249.79	86	48.51	0.35
maximum N	3.00*** -12.25*** mmN	270.41	86	20.41	0.18
TN:TP	3.03*** -0.03*** TN:TP	273.64	86	16.57	0.15
Mean depth integrated T	0.32 + 0.13* DI MT	282.53	86	6.72	0.06

Mixed Models			Random intercept coefficients			Random slope coefficients		
		AIC	AB	BC	ON	AB	BC	ON
TN	-1.50 + 1.27 log TN	216.79	-1.79	-2.38	4.18	0.82	1.1	-1.92
TKN	-2.37 + 1.55 log TKN	205.9	-2.27	-2.93	5.21	1	1.28	-2.28
TP	0.70 +1.07 log TP	216.88	-0.16	-0.21	0.37	0.46	0.59	-1.05
Average N	2.86 – 14.17 amN ***	223.9	0.53	0.14	-0.67			
Aug Surf T	4.96 – 0.14 Aug Surf T ***	224.29	0.58	0.22	-0.81			
Conductivity	1.99 + 0.00073 Cond	240.57	0.69	0.22	-0.91			
Mean Surf T	2.57 -0.03 Surf T	237.89	0.74	0.24	-0.99			
maximum N	2.29 -1.86 mmN	230.14	0.77	0.22	-0.98			
TN:TP	2.43 -0.008 TN:TP	240.98	0.73	0.25	-0.98			
Mean depth integrated T	1.25 + 0.07 DI MT	235.11	0.75	0.27	-1.02			

Table 3: Cyanobacterial traits. Bloom formers, genera characterized by the presence of gas vacuoles or heterocysts as defined by Komarek. Facultative fixers as defined by Bergman (1997). Potentially toxic species defined by Cronberg and Annadotter (2006). Genera in dark grey are dominant in all regions and species in light grey are dominant in at least one region (see Figure 2)

	Genera	Bloom Formers	Gas vacuoles	Heterocystous	Facultative Fixers	Toxin-producing potential
Chroococcales	*Aphanothece*					
	Chroococcus					
	Gomphosphaeria					x
	Microcystis	x	x			x
	Merismopedia					
	Coelosphaerium		x			x
	Synechococcus					x
	Aphanocapsa					
Nostacales	*Anabaena*	x	x	x		x
	Aphanizomenon	x	x	x		x
Oscillatoriales	*Pseudanabaena*		x		x	x
	Oscillatoria	x			x	
	Phormidium				x	
	Lyngbya				x	x

Figures

Figure 1: Biological, physical and chemical characteristics for Alberta (AB), British Columbia (BC) and Ontario (ON) lakes. Differences were tested through ANOVA and post-hoc Tukey tests. Significant grouping of the data shown as overlying grey shading.

Figure 2: Phycological characterization of regional lakes. A) Average relative abundance (%) and absolute abundance (μg L^{-1}) of phytoplankton groups for Alberta (AB) and Ontario (ON). B) Average relative abundance of cyanobacterial general for all regions.

Figure 3: Cyanobacterial biomass linear models developed for nutrient predictors (total Kjeldahl nitrogen, total nitrogen, total phosphorus, N:P ratio), chemical predictors (pH, Conductivity) and temperature-related predictors (seasonal average thermocline stability, seasonal maximal thermocline stability, seasonal average surface water temperature, seasonal average depth integrated water temperature, average August surface water temperature). Regression lines are shown with 95% confidence interval. See table 2 for equations and model descriptors.

Figure 4: Correlation matrix of the predictive variables considered for cyanobacterial biomass. On the left, the biplots are shown and the diagonal shows

the distribution of each variable. Correlation coefficients are shown on the right.

Figure 5: Cyanobacterial mixed-effects models developed for the best six predictors found through linear modeling (see Table 2). Model for pH is not shown as the linear fitted model was selected as the best fitting model for this variable. Random intercept and random slope models shown for TKN, TN and TP. Random intercept models are shown for amN, average August surface water temperature and Conductivity. Random components of the models are shown as thin lines for Alberta (AB; black), British Columbia (BC; dotted) and Ontario (ON; grey). The thick dashed line indicates a non-significant fixed effect whereas the solid thick line indicates a significant fixed effect.

Figure 6: Canonical correspondance analysis (CCA) for Alberta lakes. Shown in green are the Oscillatoriates, in yellow the Chroococcales, in blue the Nostocales and in purple the Synechoccales.

Figure 1

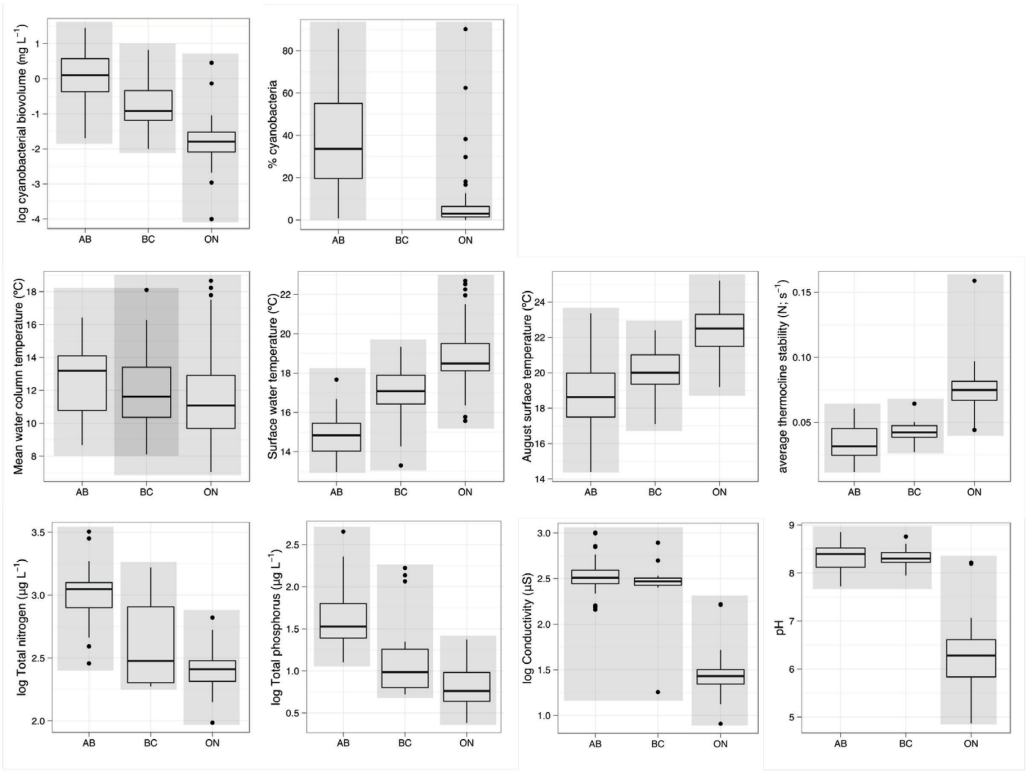

log cyanobacterial biovolume (mg L⁻¹)
% cyanobacteria
Mean water column temperature (ºC)
Surface water temperature (ºC)
August surface temperature (ºC)
average thermocline stability (N, s⁻¹)
log Total nitrogen (µg L⁻¹)
log Total phosphorus (µg L⁻¹)
log Conductivity (µS)
pH
AB
BC
ON

Figure 2

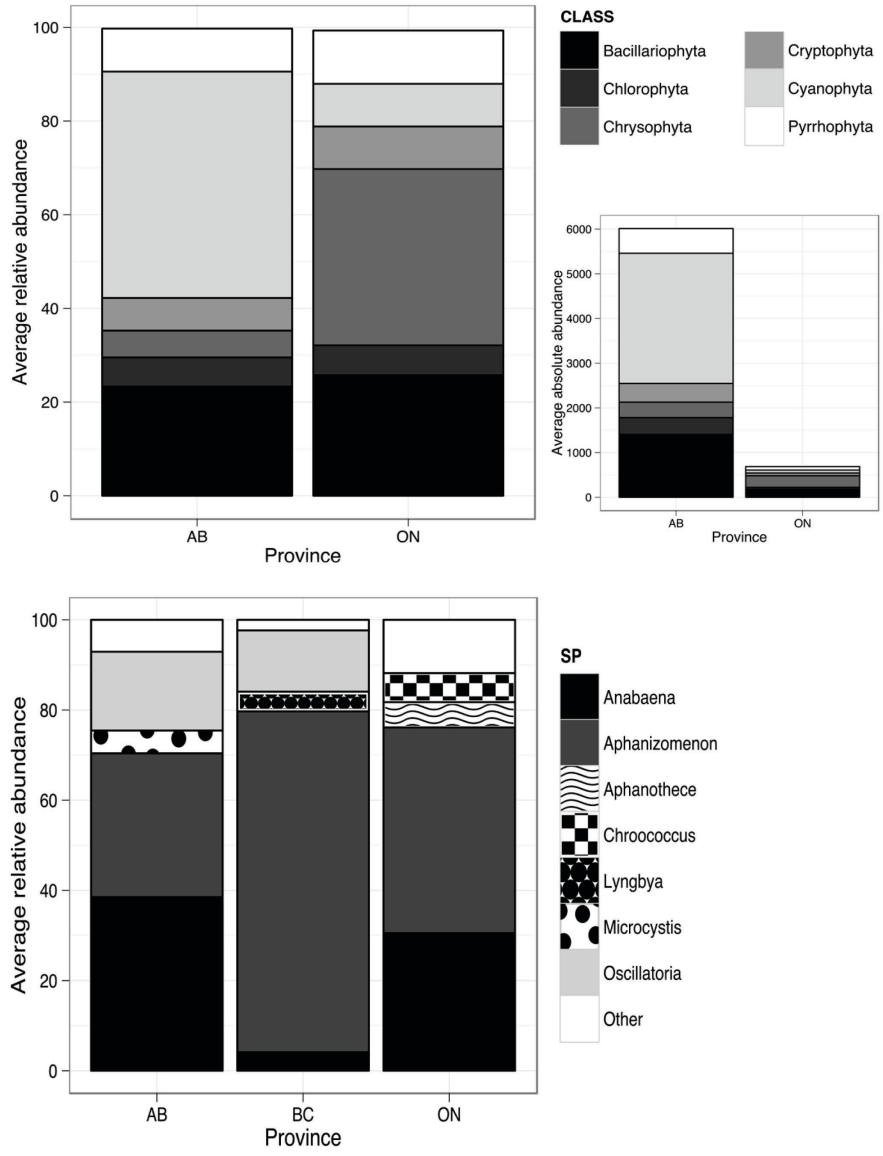

Average relative abundance
100
80
60
40
20
0
AB
ON
Province
CLASS
Bacillariophyta
Chlorophyta
Chrysophyta
Cryptophyta
Cyanophyta
Pyrrhophyta
Average absolute abundance
6000
5000
4000
3000
2000
1000
0
AB
ON
Province
Average relative abundance
100
80
60
40
20
0
AB
BC
ON
Province
SP
Anabaena
Aphanizomenon
Aphanothece
Chroococcus
Lyngbya
Microcystis
Oscillatoria
Other

Figure 3

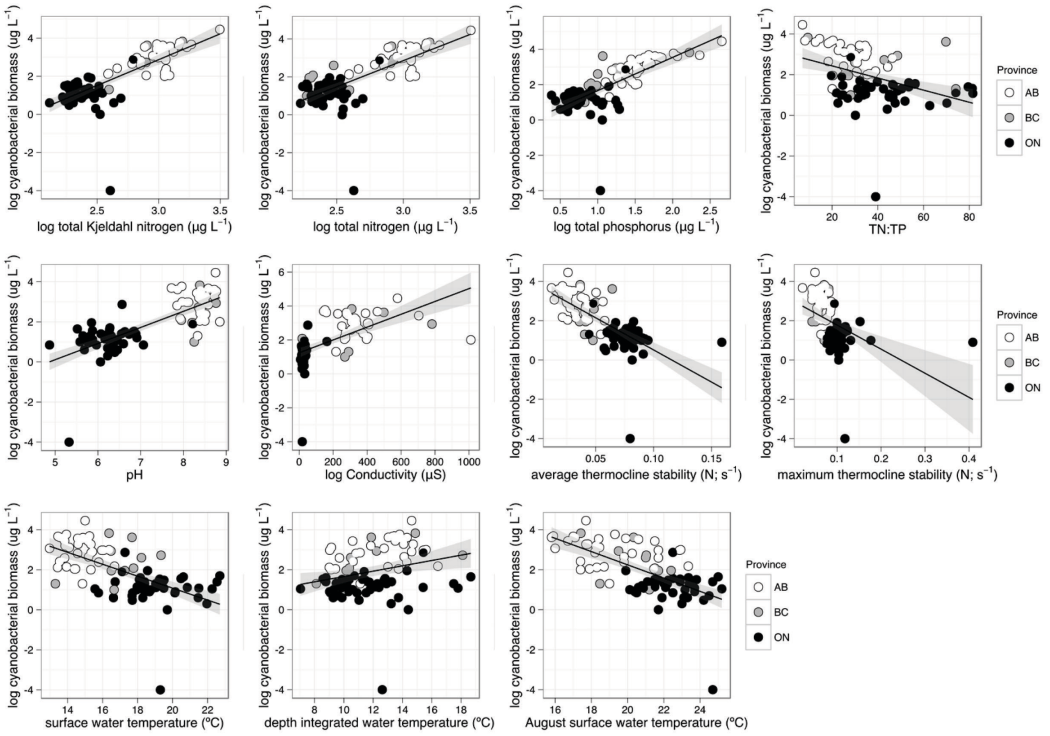

log cyanobacterial biomass (ug L^{-1})
log total Kjeldahl nitrogen (µg L^{-1})
log total nitrogen (µg L^{-1})
log total phosphorus (µg L^{-1})
TN:TP
pH
log Conductivity (µS)
average thermocline stability (N; s^{-1})
maximum thermocline stability (N; s^{-1})
surface water temperature (°C)
depth integrated water temperature (°C)
August surface water temperature (°C)
Province
AB
BC
ON

Figure 4

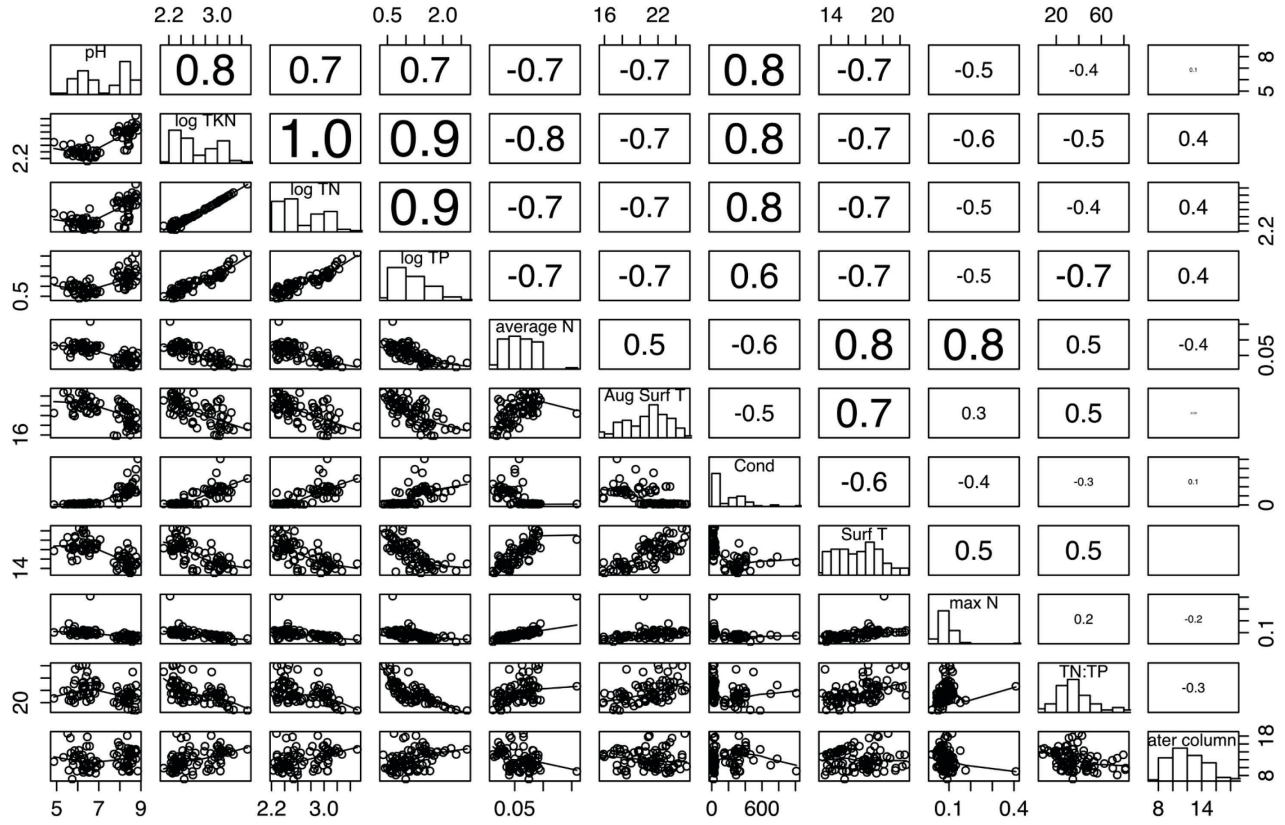

pH
log TKN
log TN
log TP
average N
Aug Surf T
Cond
Surf T
max N
TN:TP
ater column
0.8
0.7
0.7
-0.7
-0.7
0.8
-0.7
-0.5
-0.4
1.0
0.9
-0.8
-0.7
0.8
-0.7
-0.6
-0.5
0.4
0.9
-0.7
-0.7
0.8
-0.7
-0.5
-0.4
0.4
-0.7
-0.7
0.6
-0.7
-0.5
-0.7
0.4
0.5
-0.6
0.8
0.8
0.5
-0.4
-0.5
0.7
0.3
0.5
-0.6
-0.4
0.5
0.5
0.2
-0.3

Figure 5

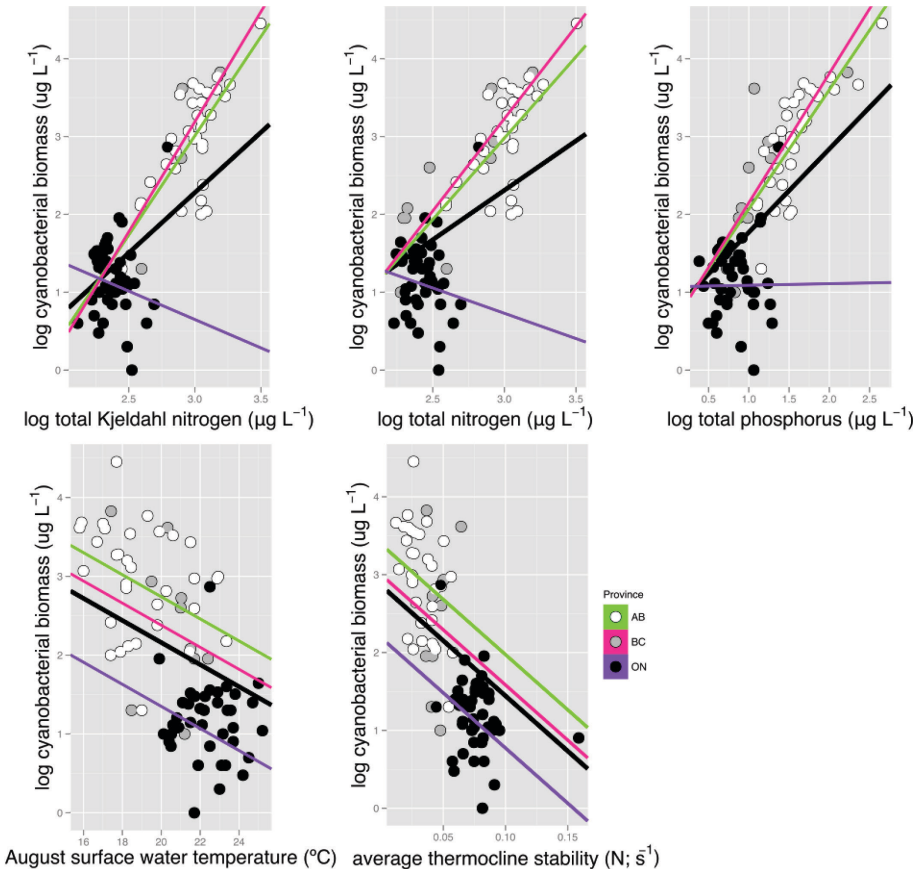
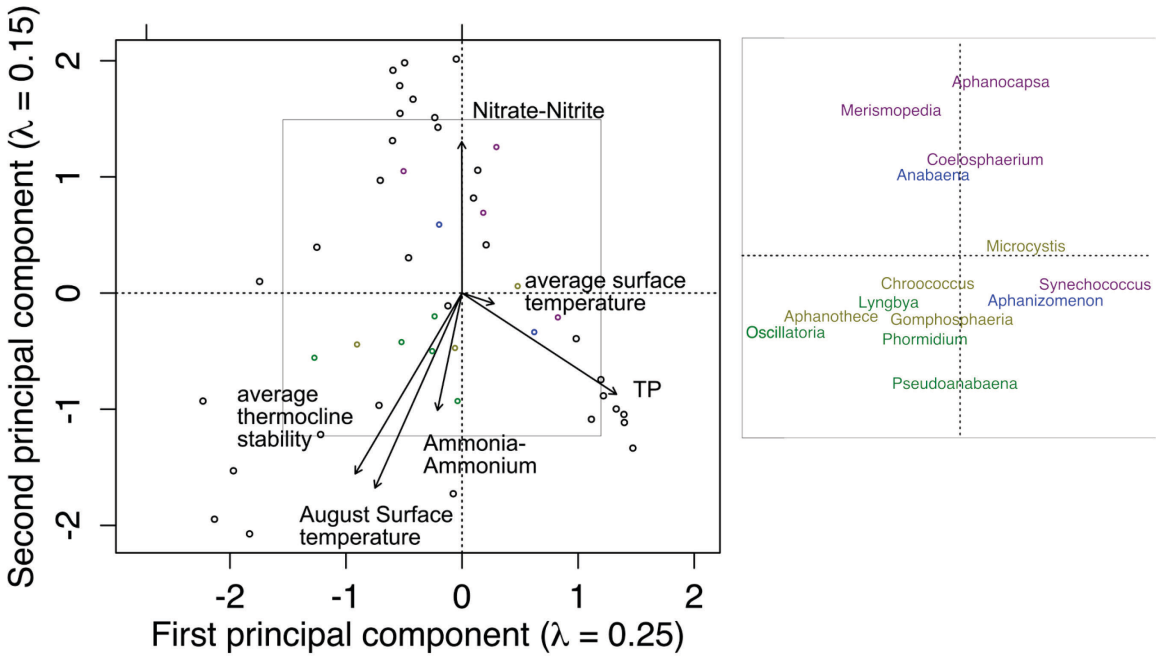

log cyanobacterial biomass (ug L^{-1})
log total Kjeldahl nitrogen (µg L^{-1})
log total nitrogen (µg L^{-1})
log total phosphorus (µg L^{-1})
August surface water temperature (°C)
average thermocline stability (N; s^{-1})
Province
AB
BC
ON

Figure 6


Second principal component (λ = 0.15)
First principal component (λ = 0.25)
Nitrate-Nitrite
average surface temperature
TP
Ammonia-Ammonium
average thermocline stability
August Surface temperature
Aphanocapsa
Merismopedia
Coelosphaerium
Anabaena
Microcystis
Chroococcus
Synechococcus
Lyngbya
Aphanizomenon
Aphanothece
Gomphosphaeria
Oscillatoria
Phormidium
Pseudoanabaena

Conclusion

My general thesis objectives were to quantify the effect of temperature and other environmental variables in promoting cyanobacterial biomass in North American lakes and test whether these effects varied across regions and lake-system types. These objectives were tackled by conducting advanced analyses using two different datasets; each of which offered its own strengths and limitations.

In chapter 1, I produced cyanobacterial biomass models with the largest dataset analyzed to date. My results from this chapter provide strong empirical support for ideas put forward from smaller-scale lab studies and anecdotal observations that temperature, in addition to nutrients, has a positive and direct effect on cyanobacterial biomass. This suggests that under a warming climate with increased surface water temperatures we might expect that in the future cyanobacteria will represent a greater fraction of the total algal biomass. Nutrients were found to mainly favour cyanobacterial biomass through their impact on total phytoplankton biomass. Previous studies have shown that the relative abundance of cyanobacteria increases as a function of total phytoplankton biomass because some genera of this group outcompete others for nutrients and light (Watson et al. 1997; Scheffer et al. 1997). Interestingly, nitrogen concentration was a significantly better nutrient predictor than phosphorus, which has often been assumed to be the limiting nutrient. This is assumption is commonly held for cyanobacteria because some taxa fix atmospheric di-nitrogen. However, there is an emerging body of work finding that contrary to what was long assumed, di-nitrogen-fixation in lakes often cannot compensate significantly for nitrogen

deficiencies (Scott and McCarthy 2010; Lewis et al. 2011). The energetic expenditure of di-nitrogen fixation might be too high under the low light conditions at high phytoplankton biomass and which might be further exacerbated by higher nitrogen-requirements of di-nitrogen fixing species (Klausmeier et al. 2004).

Given that it is well known that snapshot samples are noisier than seasonally-integrated data (Prairie 1995), the Canadian dataset used in chapter two allowed me to us to address one of the key limitations of the NLA dataset used in chapter 1. As expected, I found that nutrient models developed in chapter 2 explained much more of the variance that those presented in chapter 1. In fact, the pan-Canadian models, even with slightly different sampling and counting methods across regions, are comparable to models developed in previous studies using seasonally-integrated data. Similar to chapter 1, I found that lake water nitrogen concentration was again a better predictor than phosphorus.

The analysis of data presented in chapter 2 also provides key insights for agencies trying to ensure water quality: how do the models from one region compare to another? My analysis clearly shows that a strong similarity between British Columbia and Alberta lakes, but a clear distinction from Ontario lakes. Based on the available dataset, Ontario lakes spanned a relatively limited nutrient range, and thus more eutrophic lakes need to be included in the analysis before I can make strong conclusions regarding regional differences. This is something I hope to do in the future as some more nutrient rich lakes can be found within Ontario (although in general they are not as abundant as in Alberta).

Overall, empirical models are powerful in their ability to make broad

generalized statements as well as inform future scenarios. If we hope to address the challenges of our future in regard to the availability and management of the freshwater resources we need to be able to adequately quantify the consequences of the combined effects of nutrient enrichment and warming temperatures. This will require continued monitoring as well as the compilation of previously-collected data. The latter requires the collaboration of academics, government scientists and community scientists. Given that cyanobacteria reports are increasing in many parts of the world, it is critical that all players work collectively to effectively protect freshwaters, one of the world's most valuable and vulnerable resources.

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Appendix A : Average Genera and Species cell volumes. Dimensions taken from Cronberg and Annodotter 2006, Komárek and Anagnostidis 1998, 2008 and additional published sources in some cases. See methods Chapter 1 for details.

Genera	μm^3 $cell^{-1}$
Anabaena	124.2
Anabaenopsis	84.9
Arthrospira	56.1
Borzia	29.8
Calothrix	143.2
Chamaesiphon	115.2
Chroococcus	123.6
Coelomoron	14.8
Cyanosarcina	448.9
Cylindrospermopsis	76.7
Dactylococcopsis	108.6
Eucapsis	14.1
Geitlerinema	16.8
Gloeocapsa	6.4
Gloeothece	1.9
Gomontiella	182.5
Gomphosphaeria	74.2
Heteroleibleinia	2.6
Homoeothrix	10.9
Jaaginema	10.9
Leptolyngbya	5.7
Limnothrix	24.2
Nodularia	804.2
Oscillatoria	434.1
Phormidium	141.4
Planktolyngbya	4.9
Plectonema	1282.9
Romeria	5.0
Schizothrix	6.6
Snowella	8.1
Stichosiphon	230.9
Synechococcus	26.6
Trichodesmium	152.0
Woronichinia	61.8

Species	μm^3 $cell^{-1}$
Anabaena *affinis*	90.3
Anabaena *circinalis*	565.1
Anabaena *flosaquae*	117.2
Anabaena *lemmermannii*	72.0
Anabaena *macrospora*	181.8
Anabaena *smithii*	716.3
Anabaena *spiroides*	333.9
Anabaena *subcylindrica*	57.7
Anabaena *torulusa*	44.3
Anabaena *viguieri*	160.1
Anabaena *wisconsinense*	56.4
Anabaenopsis *elenkinii*	152.7
Aphanizomenor *aphanizomenoides*	159.0
Aphanizomenor *flosaquae*	185.2
Aphanizomenor *sp.*	38.1
Aphanocapsa *delicatissima*	0.2
Aphanocapsa *elachista*	3.3
Aphanocapsa *grevilei*	48.4
Aphanocapsa *holsatica*	0.5
Aphanocapsa *sp.*	2.2
Aphanothece *clathrata*	1.1
Aphanothece *sp.*	2.5
Chroococcus *dispersus*	29.6
Chroococcus *limneticus*	592.7
Chroococcus *microscopicus*	0.3
Chroococcus *minimus*	6.8
Chroococcus *minor*	22.4
Chroococcus *minutus*	193.4
Coelosphaerium *kuetzingianum*	13.1
Coelosphaerium *naegelianum*	28.3
Coelosphaerium *sp.*	4.3
Cuspidothrix *issatschenkoi*	72.2
Dactylococcopsis *acicularis*	2748.9
Dactylococcopsis *fascicularis?*	10.0
Gomphosphaeria *aponina*	229.2
Gomphosphaeria *virieuxii*	40.1
Homoeothrix *janthina*	3.5
Lemmermanniella *flexa*	5.1
Leptolyngbya *cartilaginea*	10.2

Species	μm^3 $cell^{-1}$
Lyngbya *contorta*	6.3
Lyngbya *limnetica*	2.2
Lyngbya *majuscula*	1705.7
Lyngbya *sp.*	398.8
Merismopedia *glauca*	47.7
Merismopedia *punctata*	16.9
Merismopedia *sp.*	22.4
Merismopedia *tenuissima*	0.5
Microcystis *aeruginosa*	65.4
Microcystis *firma*	12.1
Microcystis *flosaquae*	36.1
Microcystis *ichthyoblabe*	9.2
Microcystis *smithii*	44.6
Microcystis *sp.*	40.2
Microcystis *wesenbergii*	87.1
Oscillatoria *contorta*	434.1
Oscillatoria *limosa*	577.0
Oscillatoria *sancta*	645.4
Oscillatoria *tenuis*	148.2
Oscillatoria *Utermoehlii*	33.1
Phormidium *granulatum*	33.7
Phormidium *tenue*	61.5
Planktolyngbya *contorta*	4.9
Planktolyngbya *limnetica*	9.5
Planktothrix *agardhii*	63.8
Planktothrix *sp.*	80.5
Pseudanabaena *moniliformis*	41.9
Pseudanabaena *sp.*	9.2
Raphidiopsis *sp.*	70.9
Rhabdoderma *lineare*	15.6
Rhabdoderma *sp.*	27.8
Rhabdoglea *smithii*	17.7
Rhabdoglea *sp.*	108.6
Snowella *atomus*	0.5
Snowella *lacustris*	12.4
Spirulina *laxa*	10.9
Synechococcus *linearis*	27.8
Synechococcus *minutus*	79.5
Synechocystis *sp.*	53.4

Appendix B : Lake parameters for Canadian lakes used in Chapter 2. Unless otherwise stated, values represent seasonal averages.

Lake	Province	Year	Latitude	Longitude	Elevation (m)	Area (ha)	Volume (m^3*10^5)	Mean depth (m)	Max depth (m)
Axe	ON	2005	45° 23'	79° 30'	317.5	264	66.2	2.5	15.0
Baptiste North	AB	1985	54° 45'	113° 33'	578.52	507	281	5.6	15.5
Baptiste South	AB	1985	54° 45'	113° 33'	578.52	474	565	11.9	27.5
Basshaunt	ON	1984	45° 07'	78° 28'	403.9	47.3	36.6	7.7	24.0
Bat	ON	2004	45° 35'	78° 31'	408.4	2.33	0.69	2.9	8.3
Battle	AB	1984	52° 58'	114° 11'	836.72	456	316	6.9	13.1
Beaver	AB	1986	54° 43'	111° 37'	559.27	3310	2340	7.1	15.2
BigPorcupine	ON	2005	45° 27'	78° 37'	480	235	177.4	7.5	30.5
Bigwind	ON	1983	45° 03'	79° 03'	319	111	118	10.7	32.0
Blue Chalk	ON	1976	45° 12'	78° 56'	343.5	52.35	44.68	8.5	23.0
Bonnechere	ON	2005	45° 28'	78° 35'	480	105	67	6.4	21.4
Bonnie	AB	1983	54° 09'	111° 52'	639.02	377	117	3.1	6.1
Bouchie	BC	2007	53° 2'	122° 37'	689	127.8		3.8	7.3
Bourque	AB	1981	54° 40'	110° 32'		497		8.3	27.4
Buck	ON	1983	45° 23'	79° 00'	376	40.3	43.9	10.9	30.0
Buck	AB	1984	53° 00'	114° 45'	882.03	2540	1580	6.2	12.2
Chimney	BC	1997	51° 54'	121° 57'	914	431		8.7	19.5
Chub	ON	1976	45° 13'	78° 59'	371	34.41	30.42	8.9	27.0
CinderEast	ON	2005	45° 04'	78° 56'	332	50.1	50.7	10.1	36.5
CinderWest	ON	2005	45° 13'	78° 59'	332	26.9	12.8	4.8	16.0
Clear	ON	2005	45° 11'	78° 43'	368	88.4	109.1	12.4	33.0
Coal	AB	1985	53° 08'	113° 21'	702.06	1090	388	3.5	5.5
Cradle	ON	2005	45° 28'	78° 35'	472.4	17.89	22.25	12.4	33.3
Crosson	ON	1983	45° 05'	79° 02'	332	56.74	52.16	9.2	25.0
Crystal	ON	2005	45° 23'	78° 29'	480.1	41.02	17.77	4.3	17.1
Delano	ON	1983	45° 31'	78° 36'	449.6	23.9	17.04	7.1	18.6
Dickie	ON	1976	45° 09'	79° 05'	354.5	93.6	46.65	5.0	12.0
Dragon Lake	BC	2007	52° 56'	122° 25'	762	658		5.8	8.5
Driedmeat	AB	1984	52° 52'	112° 45'	684.44	1650	419	2.2	3.7
Ethel	AB	1983	54° 32'	110° 21'	540.75	490	322	6.6	30.0
Fawn	ON	2004	45° 10'	79° 15'	297	85.8	30.2	3.5	7.9
Glen	ON	1983	45° 08'	78° 30'	358	16.3	11.8	7.2	15.0
Hamer	ON	2004	45° 14'	79° 48'	236	35.21	11.63	3.3	8.5
Harp	ON	1976	45° 23'	79° 08'	327	71.38	95.07	13.3	37.5
Healey	ON	2004	45° 05'	79° 11'	307.5	122	33.7	2.8	7.0
Heney	ON	1980	45° 08'	79° 06'	345.5	21.37	7.05	3.3	5.8
Horse Lake	BC	2006	51° 35'	121° 9'	914	1162		15.2	34.4
Iosegun	AB	1985	54° 28'	116° 50'	744.92	1340	555	4.1	11.2
Island	AB	1984	54° 51'	113° 32'	601	781	292	3.7	18.0
Isle	AB	1984	53° 38'	114° 44'	730.05	2300	948	4.1	7.5
Kimball	ON	2004	45° 21'	78° 41'	358.1	212.6	464.2	21.8	65.5
Lac des Iles	AB	1985	54° 26'	109° 25'					35.0
Leech	ON	1984	45° 03'	79° 06'	310.5	82	51.9	6.3	13.7
Leonard	ON	1984	45° 04'	79° 27'	264.5	195	134	6.9	15.2
Lepine Lake	AB	1985	52° 38'	105° 33'					10.0
Little Clear	ON	2004	45° 24'	79° 00'	374.5	10.9	8.9	8.1	25.0
Louisa	ON	1983	45° 28'	78° 29'	440.4	531	855.9	16.1	61.0

Lake	Province	Year	Latitude	Longitude	Elevation (m)	Area (ha)	Volume (m^3*10^5)	Mean depth (m)	Max depth (m)
Maggie	ON	2005	45° 30'	78° 52'	485	138.6	141	10.2	31.0
Marie	AB	1981	54° 38'	110° 18'	573.88	3460	4840	14.0	26.0
Mary Gregg	AB	1983	53° 7'	117° 27'					12.0
May	AB	1980	54° 43'	110° 23'					15.0
McKay	ON	2004	45° 03'	79° 10'	302	121.5	63.5	5.2	19.5
Minnie	AB	1986	54° 17'	111° 6'					23.0
Moore	AB	1981	54° 31'	110° 31'	549.6	928	774	8.3	26.0
Moot	ON	1984	45° 09'	79° 10'	335.5	46.2	12.4	2.7	7.9
Nakumun	AB	1984	53° 53'	114° 12'	682.48	354	158	4.5	8.0
North Buck	AB	1986	54° 41'	112° 32'	608.57	1900	473	2.5	6.1
Nunikani	ON	1984	45° 12'	78° 44'	373	116	91.7	7.9	24.0
Okanagan (Armstrong)	BC	1996							55.0
Okanagan (Central)	BC	1997							55.0
Okanagan (Kelowna DS)	BC	1997							90.0
Okanagan (Kelowna US)	BC	1997							146.0
Okanagan (North)	BC	1997							225.0
Okanagan (Squally Pt)	BC	1997							115.0
Opinicon	ON	1991	44° 33'	76° 20'		780	383	4.9	9.0
Pearceley	ON	2005	45° 42'	79° 30'	358.4	44.14	20.82	4.7	8.1
Pierce Lake	AB	1985	53° 24'	106° 22'					40.0
Pincher	ON	2005	45° 34'	78° 51'	510.5	42.06	25.48	6.1	15.5
Plastic	ON	1982	45° 11'	78° 50'	376.4	32.14	25.24	7.9	16.3
Red Chalk East	ON	1979	45° 11'	78° 57'	343	13.05	7.48	5.7	19.0
Red Chalk Main	ON	1980	45° 11'	78° 57'	343	44.08	73.52	16.7	38.0
Sherborne	ON	1984	45° 11'	78° 47'	357	252	240.9	9.6	35.1
Skeleton North	AB	1986	54° 37'	112° 44'	623.77	789	514	6.5	17.0
Skeleton South	AB	1986	54° 37'	112° 44'	623.77	789	514	6.5	17.0
Smoke	ON	1983	45° 31'	78° 41'	421.2	679	1099	16.2	55.0
Solitaire	ON	1983	45° 23'	79° 01'	374.5	124	164	13.3	31.0
St-Anne East	AB	1985	53° 42'	114° 25'	723.21	5450	2630	4.8	9.0
St-Anne West	AB	1985	53° 42'	114° 25'	723.21	5450	2630	4.8	9.0
Sturgeon East	AB	1985	55° 06'	117° 32'	677.2	4910	2660	5.4	9.5
Sturgeon West	AB	1984	55° 06'	117° 32'	677.2	4910	2660	5.4	9.5
Timberwolf	ON	1983	45° 41'	78° 48'	419	167	124	7.4	20.4
Touchwood	AB	1986	54° 49'	111° 24'	630.5	2900	4300	14.8	40.0
Tucker	AB	1982	54° 32'	110° 36'	553.7	665	190	2.9	7.5
Upper Rock	ON	1990	44° 33'	76° 30'		70	161	20.5	44.5
Wabamun East	AB	1981	53° 33'	114° 36'	724.7	8180	5130	6.3	11.0
Wabamun Moonlight	AB	1981	53° 33'	114° 36'	724.7	8180	5130	6.3	11.0
Wabamun West	AB	1981	53° 33'	114° 36'	724.7	8180	5130	6.3	11.0
Walker	ON	2004	45° 23'	79° 05'	359.5	68.2	42.1	6.2	17.0
Westward	ON	1983	45° 29'	78° 45'	428.5	63	129.5	20.5	44.0
Williams Lake	BC	2006	52° 4'	120° 4'	565	720		12.0	24.0
Young	ON	2004	45° 13'	79° 33'	241.5	105.9	127.4	12.0	21.1

Lake	Thermocline stability (Brunt-Väisälä Frequency index ; s^{-1})	Maximal thermocline stability (Brunt-Väisälä Frequency index ; s^{-1})	Depth integrated water temperature (ºC)	Surface water temperature (ºC)	August surface water temperature (ºC)
Axe	0.08	0.12	12.62	19.30	24.70
Baptiste North	0.04	0.06	11.84	13.86	18.25
Baptiste South	0.04	0.07	9.15	14.10	18.45
Basshaunt	0.08	0.09	10.21	19.20	20.80
Bat	0.08	0.10	11.52	17.72	20.50
Battle	0.03	0.05	14.12	15.20	19.80
Beaver	0.03	0.06	14.63	15.42	18.20
BigPorcupine	0.09	0.10	9.88	21.50	23.70
Bigwind	0.06	0.12	8.77	16.72	22.90
Blue Chalk	0.08	0.11	12.75	19.23	21.72
Bonnechere	0.09	0.10	10.30	22.26	25.20
Bonnie	0.03	0.08	13.73	14.39	21.45
Bouchie	0.04	0.07	14.88	16.37	17.42
Bourque	0.06	0.09	9.04	16.05	21.70
Buck	0.08	0.12	9.88	18.10	21.50
Buck	0.03	0.06	13.62	14.70	18.40
Chimney	0.05	0.07	12.23	16.48	19.50
Chub	0.09	0.13	10.61	18.76	20.52
CinderEast	0.07	0.09	7.04	15.57	
CinderWest	0.07	0.08	9.09	15.77	
Clear	0.09	0.11	13.25	22.54	24.70
Coal	0.01	0.02	13.34	13.45	17.00
Cradle	0.08	0.10	9.27	21.46	23.30
Crosson	0.10	0.18	9.30	18.33	23.17
Crystal	0.09	0.10	13.23	21.96	23.00
Delano	0.08	0.11	10.32	18.68	23.70
Dickie	0.08	0.15	14.31	18.57	19.90
Dragon Lake	0.04	0.09	18.11	19.34	21.03
Driedmeat	0.03	0.05	14.63	15.00	17.70
Ethel	0.04	0.09	9.70	13.83	21.70
Fawn	0.07	0.08	15.41	19.05	20.60
Glen	0.07	0.10	11.39	17.13	
Hamer	0.08	0.10	14.40	19.70	21.70
Harp	0.08	0.12	10.71	22.70	
Healey	0.07	0.09	17.79	19.50	20.90
Heney	0.04	0.08	17.50	18.41	23.57
Horse Lake	0.04	0.07	8.12	13.30	18.47
Iosegun	0.04	0.06	13.44	15.25	15.90
Island	0.03	0.06	14.29	15.78	19.80
Isle	0.02	0.06	14.31	14.88	17.10
Kimball	0.16	0.41	9.03	20.15	20.40
Lac des Iles	0.04	0.08	10.63	13.55	17.40
Leech	0.07	0.08	12.16	17.98	21.50
Leonard	0.07	0.10	12.90	18.23	22.20
Lepine Lake	0.03	0.08	13.01	13.94	18.70
LittleClear	0.08	0.10	8.58	19.27	22.90
Louisa	0.06	0.08	9.48	18.30	22.00

Lake	Thermocline stability (Brunt-Väisälä Frequency index ; s^{-1})	Maximal thermocline stability (Brunt-Väisälä Frequency index ; s^{-1})	Depth integrated water temperature (ºC)	Surface water temperature (ºC)	August surface water temperature (ºC)
Maggie	0.08	0.10	12.82	20.48	22.50
Marie	0.04	0.07	10.83	14.57	20.25
Mary Gregg	0.05	0.06	11.12	14.85	19.00
May	0.05	0.07	12.46	15.69	18.80
McKay	0.07	0.10	11.73	19.30	21.40
Minnie	0.06	0.07	9.12	15.33	17.40
Moore	0.05	0.08	10.60	15.17	21.50
Moot	0.06	0.10	13.73	16.62	21.90
Nakumun	0.03	0.05	14.04	14.81	20.60
North Buck	0.03	0.06	14.73	15.33	17.70
Nunikani	0.06	0.08	11.04	17.70	24.20
Okanagan (Armstrong)	0.05	0.06	12.08	18.18	20.50
Okanagan (Central)	0.05	0.06	10.47	18.22	21.00
Okanagan (Kelowna DS)	0.04	0.04	10.16	16.50	22.40
Okanagan (Kelowna US)	0.04	0.05	10.34	17.27	21.70
Okanagan (North)	0.04	0.05	10.38	17.77	21.50
Okanagan (Squally Pt)	0.05	0.07	10.08	16.66	21.20
Opinicon	0.01	0.07	18.90	19.33	22.00
Pearceley	0.07	0.11	18.67	20.62	25.00
Pierce Lake	0.04	0.08	9.01	13.43	18.30
Pincher	0.09	0.11	12.40	20.84	22.10
Plastic	0.07	0.11	11.79	17.95	20.12
Red Chalk East	0.09	0.12	11.46	19.51	22.25
Red Chalk Main	0.08	0.11	8.78	18.16	23.36
Sherborne	0.07	0.09	9.63	17.68	24.50
Skeleton North	0.05	0.07	11.11	15.35	18.20
Skeleton South	0.02	0.04	14.08	14.60	17.80
Smoke	0.06	0.08	10.36	18.12	23.80
Solitaire	0.08	0.12	11.25	18.12	21.60
St-Anne East	0.01	0.04	12.75	12.97	16.00
St-Anne West	0.02	0.04	13.51	13.83	16.70
Sturgeon East	0.02	0.04	13.04	13.57	15.80
Sturgeon West	0.02	0.07	13.81	13.93	19.30
Timberwolf	0.07	0.10	12.29	19.03	23.40
Touchwood	0.04	0.06	9.43	14.45	17.90
Tucker	0.02	0.06	13.92	14.58	19.90
Upper Rock	0.06	0.09	13.47	16.67	23.00
Wabamun East	0.03	0.07	15.43	15.95	22.87
Wabamun Moonlight	0.02	0.06	16.42	16.68	23.35
Wabamun West	0.02	0.06	15.61	16.37	22.93
Walker	0.07	0.08	11.62	18.40	21.10
Westward	0.07	0.12	9.87	18.30	23.10
Williams Lake	0.06	0.08	11.87	17.68	20.33
Young	0.08	0.10	10.89	20.13	22.50

Lake	Cyano biomass (µg L^{-1})	Phyto biomass (µg L^{-1})	Total P (µg L^{-1})	Total N (µg L^{-1})	NH^4-NH^3 (µg L^{-1})	NO^3-NO^2 (µg L^{-1})	TKN (µg L^{-1})	Specific Cond. (µS cm^{-1})	pH
Axe	0.00	1.182	10.87	424.50	36.50	30.00	404.50	18.33	5.33
Baptiste North	1.58	5.53	51.20	1164.29	19.57	40.29	1125.71	334.71	8.36
Baptiste South	1.30	7.01	44.80	1134.29	34.57	21.50	1117.14	329.29	8.41
Basshaunt	0.02	0.402	6.22	302.25	3.50	28.50	273.75	37.15	6.91
Bat	0.01	2.737	18.47	496.33	28.67	3.67	492.67	8.10	4.87
Battle	0.44	1.04	33.25	610.00	13.67	4.33	608.33	352.33	8.40
Beaver	0.80	3.24	33.20	1146.00	31.60	15.00	1140.00	409.80	8.50
BigPorcupine	0.01	0.291	2.74	223.40	14.50	68.00	211.25	18.72	6.39
Bigwind	0.03	1.031	6.68	235.67	5.83	48.17	187.50	29.67	6.55
Blue Chalk	0.03	0.37	7.79	192.12	13.63	16.82	175.31	30.91	6.61
Bonnechere	0.01	0.252	4.53	204.25	15.00	17.50	249.00	17.95	6.28
Bonnie	0.11	1.23	34.03	1231.67	28.33	7.83	1225.00	397.00	8.50
Bouchie	6.68		167.42	1575.83	437.33	19.00	1556.67	309.75	8.38
Bourque	0.94	12.62	20.28	682.50	38.00	4.00	664.00	337.33	8.12
Buck	0.03	0.384	5.31	246.60	6.80	44.60	202.00	29.96	6.84
Buck	3.46	10.23	42.08	770.00	7.33	3.00	770.00	227.83	8.42
Chimney	0.86		17.41	845.45	35.41	12.86		781.95	8.76
Chub	0.01	0.83	11.36	282.01	17.82	32.36	249.65	30.75	5.78
CinderEast	0.01	0.372	9.90	343.33	33.33	60.00	283.33	20.07	5.74
CinderWest	0.01	0.918	11.42	358.33	44.67	58.00	300.33	19.93	5.96
Clear	0.03	0.084	2.42	192.40	9.20	8.80	183.60	18.92	6.07
Coal	4.65	9	229.25	1868.33	166.33	30.33	1838.33	460.67	8.58
Cradle	0.00	0.338	3.56	169.40	14.80	7.60	202.25	16.88	6.29
Crosson	0.01	0.97	11.74	281.64	17.57	50.28	231.37	25.00	5.58
Crystal	0.00	0.859	8.02	354.00	21.20	46.00	308.00	16.92	6.23
Delano	0.01	0.533	5.36	241.00	5.90	22.00	219.00	29.18	6.35
Dickie	0.09	0.71	14.14	279.38	21.81	11.88	267.49	28.76	5.85
Dragon Lake	0.53		18.75	802.50	87.00	14.00	790.00	325.00	8.35
Driedmeat	28.36	31.4	452.37	3203.33	182.00	69.00	3133.33	578.83	8.75
Ethel	0.39	2.16	23.05	714.00	118.60	6.00	712.00	305.75	8.38
Fawn	0.01	0.464	17.27	376.50	14.33	27.33	349.17	26.43	6.42
Glen	0.08	3.516	13.85	337.75	43.13	56.50	281.25	163.33	8.22
Hamer	0.00	0.375	11.52	347.67	17.67	13.33	334.33	32.63	6.06
Harp	0.05	0.75	8.23	264.60	12.78	46.20	218.40	35.55	6.28
Healey	0.01	0.642	9.67	331.00	13.33	22.00	309.00	39.40	6.45
Heney	0.02	0.37	8.53	266.15	8.14	14.96	251.19	25.62	5.65
Horse Lake	0.02		5.33	395.00	6.33	2.00	395.00	291.00	
Iosegun	4.82	5.94	48.00	980.00	29.40	22.25	966.67	144.40	7.72
Island	0.24	1.52	26.12	1158.33	28.67	15.50	1150.00	376.83	8.52
Isle	4.03	5.52	115.50	1470.00	67.50	19.00	1456.67	278.17	8.72
Kimball	0.01	0.707	4.38	204.00	10.00	38.00	166.00	22.20	6.60
Lac des Iles	0.26	1.93	18.42	461.00	5.44	2.60	460.00	273.90	8.39
Leech	0.01	0.746	9.54	310.75	9.38	12.00	298.75	32.35	6.16
Leonard	0.02	0.301	5.68	286.50	8.50	29.00	257.50	34.63	5.83
Lepine Lake	0.14	0.46	12.77	391.82	7.63	2.38	391.82	266.36	8.41
LittleClear	0.03	0.76	4.12	231.67	12.67	49.67	182.00	31.80	6.85
Louisa	0.02	0.453	3.60	293.00	6.60	105.00	188.00	28.80	6.23

Lake	Cyano biomass ($\mu g\ L^{-1}$)	Phyto biomass ($\mu g\ L^{-1}$)	Total P ($\mu g\ L^{-1}$)	Total N ($\mu g\ L^{-1}$)	NH^4-NH^3 ($\mu g\ L^{-1}$)	NO^3-NO^2 ($\mu g\ L^{-1}$)	TKN ($\mu g\ L^{-1}$)	Specific Cond. ($\mu S\ cm^{-1}$)	pH
Maggie	0.04	0.198	4.30	242.20	19.60	22.00	220.20	15.48	5.87
Marie	0.65	1.51	15.48	716.92	37.50	4.90	715.38	251.50	7.85
Mary Gregg	0.02	2.53	14.28	286.67	14.33	23.00	280.00	217.00	8.33
May	3.36	14.11		892.00	30.20	11.50	910.00	244.17	8.03
McKay	0.02	0.921	8.07	299.00	8.00	26.67	272.33	28.77	6.73
Minnie	0.10	1.4	31.67	1118.33	24.33	4.50	1116.67	1010.67	8.85
Moore	2.70	18.96	27.94	962.00	26.00	4.33	962.00	704.00	8.36
Moot	0.00	1.252	19.46	439.60	20.20	7.60	432.00	22.20	5.68
Nakumun	3.30	4.84	71.70	1691.43	23.71	2.00	1691.43	278.86	8.77
North Buck	1.87	3.87	29.67	1048.33	20.83	2.33	1048.33	326.17	8.53
Nunikani	0.00	0.277	3.99	250.00	5.00	62.50	187.50	29.23	6.39
Okanagan (Armstrong)	0.37		9.00	236.67	11.00	12.33			8.50
Okanagan (Central)	0.40		10.00	300.00	5.80	5.80			8.42
Okanagan (Kelowna DS)	0.09		9.67	196.67	5.17	30.67			8.21
Okanagan (Kelowna US)	0.09		7.50	203.33	9.50	30.67			8.20
Okanagan (North)	0.12		8.14	210.00	5.86	21.13		18.00	7.95
Okanagan (Squally Pt)	0.01		6.71	188.57	5.29	27.00		269.00	8.25
Opinicon	0.45		12.39		52.50	6.24			
Pearceley	0.04	0.436	4.75	188.83	16.00	17.50	212.60	13.30	5.52
Pierce Lake	0.13	0.44	12.63	390.91	10.14	6.27	387.27	273.45	8.45
Pincher	0.01	0.244	3.76	278.60	16.00	25.60	253.00	14.80	5.88
Plastic	0.01	0.3	5.97	201.27	11.25	11.70	189.57	22.49	5.77
Red Chalk East	0.03	0.54	7.46	348.97	76.88	21.90	327.07	32.97	6.26
Red Chalk Main	0.04	0.61	5.76	308.21	13.11	100.30	207.91	30.44	6.27
Sherborne	0.01	0.349	3.97	206.00	6.33	32.67	173.33	26.90	6.23
Skeleton North	0.71	1.78	36.33	1141.67	32.50	5.25	1140.00	323.67	8.58
Skeleton South	1.90	4.78	46.67	1320.00	37.20	4.00	1318.00	327.20	8.72
Smoke	0.03	0.649	4.89	263.33	9.33	86.67	176.67	32.98	6.63
Solitaire	0.03	0.466	5.06	176.00	6.00	3.00	173.00	29.96	6.82
St-Anne East	1.17	3.43	25.40	894.29	12.14	2.43	894.29	308.43	8.49
St-Anne West	2.74	4.77	36.20	1158.57	19.14	28.57	1128.57	287.57	8.31
Sturgeon East	4.13	5.01	58.00	1122.86	170.57	51.00	1078.57	160.14	7.86
Sturgeon West	5.84	10.89	102.69	1490.00	19.71	6.14	1484.29	152.00	7.96
Timberwolf	0.02	1.039	5.41	229.83	3.67	30.33	199.50	26.97	6.31
Touchwood	0.11	0.75	21.00	798.33	24.40	8.00	791.67	266.83	8.38
Tucker	3.69	5.57	67.09	1251.54	135.08	20.40	1236.92	390.75	8.40
Upper Rock	1.45		9.87		26.00	12.89			
Wabamun East	0.94	2.25	33.66	960.00	47.33	3.75	986.67	402.11	8.08
Wabamun Moonlight	0.15	1.01	28.67	1117.50	37.25	3.20	1117.50	404.38	7.92
Wabamun West	0.99	3.04	33.41	1000.00	58.38	3.00	1023.75	407.00	7.97
Walker	0.03	1.216	4.58	245.50	14.67	32.00	213.50	43.83	6.89
Westward	0.00	0.076	3.16	221.67	2.92	91.67	130.00	24.65	6.46
Williams Lake	4.14		11.67	814.29	17.33	14.57	804.29	498.50	8.61
Young	0.01	0.799	5.35	249.33	9.33	12.67	236.67	26.47	7.06