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# Forecasting cyanobacteria dominance in Canadian temperate lakes

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ABSTRACT

Predictive models based on broad scale, spatial surveys typically identify nutrients and climate as the most important predictors of cyanobacteria abundance; however these models generally have low predictive power because at smaller geographic scales numerous other factors may be equally or more important. At the lake level, for example, the ability to forecast cyanobacteria dominance is of tremendous value to lake managers as they can use such models to communicate exposure risks associated with recreational and drinking water use, and possible exposure to algal toxins, in advance of bloom occurrence. We used detailed algal, limnological and meteorological data from two temperate lakes in south-central Ontario, Canada to determine the factors that are closely linked to cyanobacteria dominance, and to develop easy to use models to forecast cyanobacteria biovolume. For Brandy Lake (BL), the strongest and most parsimonious model for forecasting % cyanobacteria biovolume (% CB) included water column stability, hypolimnetic TP, and % cyanobacteria biovolume two weeks prior. For Three Mile Lake (TML), the best model for forecasting % CB included water column stability, hypolimnetic TP concentration, and 7-d mean wind speed. The models for forecasting % CB in BL and TML are fundamentally different in their lag periods (BL = lag 1 model and TML = lag 2 model) and in some predictor variables despite the close proximity of the study lakes. We speculate that three main factors (nutrient concentrations, water transparency and lake morphometry) may have contributed to differences in the models developed, and may account for variation observed in models derived from large spatial surveys. Our results illustrate that while forecast models can be developed to determine when cyanobacteria will dominate within two temperate lakes, the models require detailed, lake-specific calibration to be effective as risk-management tools.



## 1. Introduction

The occurrence, frequency, magnitude and duration of cyanobacteria blooms in freshwater lakes is on the rise globally as anthropogenic activities continue to change our climate and increase nutrient concentrations (O'Neil et al., 2012; Paerl et al., 2011). Identification of factors that favour the development of cyanobacteria blooms in lakes is of vital importance for the effective management of our limited freshwater resources. Numerous limnological factors have been linked to the dominance of cyanobacteria and development of blooms in freshwater systems, including: (i) elevated nutrient concentrations, especially high phosphorus (P) (Schindler et al., 2008) and altered nitrogen to phosphorus (N:P) ratios (Posch et al., 2012; Schindler, 1977); (ii) low $CO_2$ or high pH (Shapiro, 1990); (iii) greater water column stability and algal buoyancy control (Paerl, 1988; Soranno, 1997); (iv) low underwater light (Havens et al., 1998); (v) anoxia and availability of ferrous iron (Molot et al., 2010, 2014) and (vi) top down processes related to the grazing activity of higher level organisms (DeMott et al., 1991; Rollwagen-Bollens et al., 2013).

Additionally, recent evidence has shown that blooms may be enhanced under specific meteorological conditions, such as high water temperature correlated to high air temperatures (Kosten et al., 2012; Paerl and Huisman, 2008; Taranu et al., 2012), low precipitation (Reichwaldt and Ghadouani, 2012; Romo et al., 2013), elevated solar irradiance (Zhang et al., 2012) and reduced wind speeds (Cao et al., 2006; Kanoshina et al., 2003). Among these

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factors, nutrient enrichment in particular has been associated with increases in algal biomass worldwide (Heisler et al., 2008). However, it is expected that climatic change will amplify bloom formation by increasing the geographical extent and frequency of blooms, lowering critical nutrient thresholds, and extending the seasonal duration of blooms within lakes (Johnk et al., 2008; Paerl and Huisman, 2009; Persaud et al., 2014).

Modelling cyanobacteria abundance and bloom occurrence is complex and challenging because they are affected by numerous interacting factors. For example, several studies have modelled cyanobacteria blooms in coastal systems (e.g. Wong et al., 2007), and large well studied freshwater lakes such Lake Taihu in China and Lake Windmere in the UK (e.g. Elliot, 2012; Zhang et al., 2012), but few models exist for small freshwater lakes that are common to many temperate lake districts (e.g. Elliot and Defew, 2012). In the past, predictive models based on broad, spatial surveys of numerous lakes have typically identified nutrient concentrations as the most important predictors of cyanobacteria abundance (e.g. Downing et al., 2001). More recently, however, research has indicated that both climatic variables, and limnological variables related to climate (e.g. surface water temperature), are also important predictors (Beaulieu et al., 2013; Kosten et al., 2012), and should therefore be taken into account when developing predictive and forecast models. This may be of particular importance when examining changes within lakes over time, where inter-annual differences in bloom intensity, duration, and phenology may be strongly influenced by meteorological conditions (Persaud et al., 2014). Furthermore, broad, landscape models typically have low predictive power (eg. Beaulieu et al. (2013); Downing et al. (2001); Taranu et al. (2012)) as they cannot account for small scale lake-specific parameters which may be instrumental in driving cyanobacteria dynamics.

The ability to forecast cyanobacteria dominance and bloom occurrence would be of tremendous value to lake managers. Forecast models are fundamentally different from simple predictive models in that they are based on dynamic relationships between cyanobacteria abundance, and limnological and environmental parameters over a time dimension. With such models, managers would be able to communicate exposure risks associated with recreational and drinking water use, as well as possible exposure to algal toxins, in advance of bloom occurrence. Forecast models would also be invaluable as an educational tool, providing knowledge to lake users and the general public regarding possible reasons for inter-annual differences in bloom intensity and duration, and providing clear guidance on management options for lakes experiencing blooms.

With over 2000 freshwater lakes within the Muskoka River Watershed of south-central Ontario, Canada, the Muskoka region is a focal point for tourism in Ontario and premier destination for recreational activities year round. Among the lakes in this region there are a few that experience cyanobacteria blooms on a recurring basis during the ice-free season. The factors driving cyanobacteria blooms in these temperate lakes are currently unknown. Therefore, we used algal data and numerous limnological and meteorological parameters to determine the factors that are closely linked to cyanobacteria dominance, and developed models to forecast cyanobacteria biovolume and possible bloom occurrence. Our primary goal is to develop forecast models that can be applied as a tool by resource managers to forecast bloom development, up to a month in advance. We are particularly interested in developing models that are easy to use by land managers, and assessing the differences and similarities between lake-specific models considering that the two lakes are in close proximity within the landscape.

## 2. Method

### 2.1. Study lakes

Brandy Lake (BL; 45° 06′ N, 79° 31′ W) and Three Mile Lake (TML; 45° 10′ N; 79° 27′ W) are moderately-sized, softwater lakes located 19 km apart in the Muskoka region of Ontario (Fig. 1). The watersheds of these lakes consist primarily of glacial deposits of sand, silt and clay with some organic deposits over granitic bedrock. Climatically, mean annual temperature and total precipitation for these lakes in the Muskoka region between the years 2000–2012 were 5.44 ± 0.78 °C and 1172 ± 121 mm, respectively (Environment Canada, http://www.cccma.ec.gc.ca/hccd/).

The two study lakes are different in their morphometric, chemical and physical characteristics (Table 1). Brandy Lake is much smaller, has a larger drainage ratio and faster flushing rate compared to mutli-basin TML (Table 1). BL can be classified as borderline eutrophic with epilimnetic spring total phosphorus (TP) and total nitrogen (TN) concentrations of 32.6 ± 9.80 μg $L^{-1}$ (mean ± SD) and 598 ± 67.5 μg $L^{-1}$ over the three years of study (as indicated in Table 1). BL has a relatively large (39.9 $km^2$) and wetland-dominated watershed. The watershed contains ~15% of productive wetlands and 78% of exposed bedrock (Ontario Ministry of Environment, 2006). Nutrient inputs are primarily from natural sources (due to its large drainage ratio), with an estimated 66% of the nutrients transported from the watershed into the lake originating from the wetlands (Ontario Ministry of Environment, 2006).

Three Mile Lake is classified as mesotrophic with spring total phosphorus and nitrogen concentrations of 13.8 ± 2.10 μg $L^{-1}$ and 467 ± 9.45 μg $L^{-1}$, respectively, over the three years. The watershed of TML is atypical within the Muskoka region as it supports a comparatively large agricultural community (8% of the watershed area) because pockets of the basin contain deeper soils that are more fertile compared to nearby locations. Paleoecological data suggest that deforestation was a major contributor to nutrient input into TML in the 1800s and early 1900s, however recent TP concentrations are lower than the historical peak as afforestation has occurred (Roland Hall, Department of Biology, University of Waterloo, unpublished). For this study we focussed on Hammell's Bay, the deepest (12 m) and only dimictic basin of TML. The hypolimnia of both Hammell's Bay and BL become anoxic seasonally, with dissolved oxygen concentrations less than 1 mg $L^{-1}$ by mid-summer.

### 2.2. Phytoplankton

Algal samples were collected on a biweekly and monthly basis in each lake during the ice-free period over three years. In TML the samples were collected from the deepest point in Hammell's Bay in 2006, 2007 and 2012. In BL samples were collected from the deepest location of the main basin in 2002, 2003 and 2012. Water samples were collected as unfiltered, volume-weighted, euphotic zone composites (approximated as 2 × Secchi depth) using a polyvinyl chloride (PVC) pump-and-hose system. Collected samples were fixed with 1 mL Lugol's iodine solution in the field and stored in the laboratory until enumeration.

Using an inverted microscope and Utermöhl counting chambers, algal samples were counted by the Algal Taxonomy Unit Laboratory, Ontario Ministry of the Environment (Toronto, Ontario). Subsamples were preserved with two drops of 37% formalin and concentrated to 25 mL following settling. A minimum of 300 pieces (single cells or colonies) were counted and identified mainly to the genus level, and results were expressed as biovolume. Estimates of cell volumes for each taxon were obtained by measuring the dimensions of 30–50 cells and application of the geometric formula

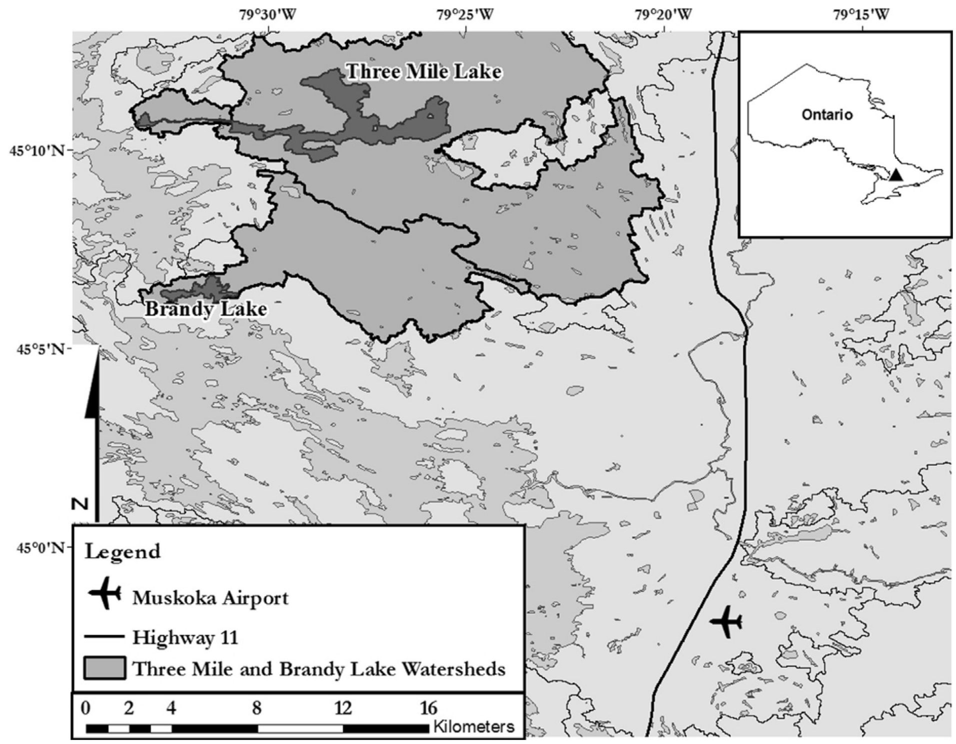


**Fig. 1.** Location of Three Mile Lake and Brandy Lake in the Muskoka River Watershed, Ontario, Canada.

best fitted to the shape of the cell. The emphasis on identification was to obtain counts of the following taxonomic groups: Chlorophytes, Cyanophytes, Chrysophytes, Cryptophytes, Bacillariophytes, Dinoflagellates and Euglenophytes. A specific gravity of one was assumed for cellular mass in the conversion of cell counts to wet weight biomass and expressed as biovolume (Hopkins and Standke, 1992).

### 2.3. Nutrients

Water samples were collected on the same collection dates as algal samples. Volume-weighted samples for epilimnetic, metalimnetic, and hypolimnetic nutrient concentrations were collected using a pump and weighted hose. Water samples were then filtered through an 80-μm filter to remove large particles and analysed using standard laboratory protocols at the Ontario Ministry of the Environment's Dorset Environmental Science Centre for total phosphorus (TP) and total nitrogen (TN = mass sum of total Kjeldahl nitrogen, nitrate and nitrite) (Ontario Ministry of the Environment, 1983). Using the chemistry data we computed single basin-wide volume-weighted nutrient concentrations and TN:TP mass ratios.

### 2.4. Physical parameters

Secchi transparency depths, and oxygen-temperature profiles measured using a YSI model 58 handheld meter, were taken concurrently with the biweekly sampling for algae and nutrients. Temperature and oxygen profiles were obtained from the surface and at 1 m intervals at the deepest location in the main basin of BL and Hammell's Bay in TML. For each sampling date, water column stability, S (g cm$^{-1}$), was calculated using temperature profiles and the Schmidt stability index formula:

$$S = \frac{1}{A_0}\sum_{z=0}^{z=m}(\rho_z - \rho^*)\left(z - z_p\right)(A_z)(\Delta z)$$

where $A_0$ is the area of a water body, $A_z$ is the lake area at depth z, $\rho_z$ is the density as calculated from temperature, $\rho^*$ is the lake's mean density, and $z_\rho$ is the depth at which the mean density is found, m is the maximum depth of the basin and Δz is the depth interval of measurements (Likens, 1985).

### 2.5. Meteorological data

Air temperature (°C), precipitation (mm), air pressure (kPa) and wind speed (km hr$^{-1}$) data were obtained from Environment Canada's National Climate Data and Information Archive for the Muskoka Airport location. This weather station is located approximately 26 km and 23 km from TML and BL, respectively (Fig. 1). To explore both short-term and any potential delayed effects we computed the mean values over 2, 3, 5, 7 and 10 days prior to the date of algal sample collection for temperature, air pressure and wind speed. For precipitation, we computed the total values over 2, 3, 5, 7 and 10 days prior to the date of algal sample collection.

### 2.6. Data analyses

Time series analyses and Pearson pairwise correlations were used to determine the important predictor variables for development of the TML and BL forecast models. We used % cyanobacteria biovolume (% CB) as the algal response variable and 27 predictor variables (Table 2: 7 limnological and 20 meteorological) in the time series analyses. The response variables were cross-correlated to the predictor variables at 1 and 2 lag time periods which represented approximately 14 and 28 days, respectively. We did not focus on longer time period lags because cross-correlations were generally not significant at lags higher than 2. Furthermore, we

**Table 1**
Selected morphological, physical and chemical characteristics of the two study lakes. Chemistry values are based on epilimnetic spring values for the three sample years.

| Lake | Brandy Lake | Three Mile Lake |
|---|---|---|
| $Z_{max}$ (m)[a] | 7.5 | 12 |
| Lake area ($km^2$) | 1.1 | 8.8[c] |
| Drainage ratio | 37:1 | 17:1 |
| Flushing rate (yr)[b] | 2.76 | 6.75 |
| Spring total phosphorus ($\mu g\ L^{-1}$) | 32.6 ± 9.80 | 13.8 ± 2.10 |
| Spring total nitrogen ($\mu g\ L^{-1}$) | 598 ± 67.5 | 467 ± 9.45 |
| Dissolved organic carbon ($mg\ L^{-1}$) | 11.8 ± 1.27 | 5.23 ± 0.15 |
| Years sampled (days sampled) | 2002 (13), 2003 (10), 2012 (11) | 2006 (12), 2007 (6), 2012 (10) |

[a] $Z_{max}$ = maximum lake depth.
[b] Average calculated using mean runoff values for the years sampled.
[c] Lake area for the entire lake, Hammell's Bay is 2.3 $km^2$.

focussed on positive lags only as our goal was to develop models which can be used to forecast cyanobacteria dominance and bloom occurrence.

The use of time series data for development of forecast models is often hampered by autocorrelation within the time series data. In our dataset there was significant autocorrelation in the cyanobacteria data for Brandy Lake (Ljung-Box Q = 21.51, $p < 0.0001$ at both lags 1 and 2), but not TML (Ljung-Box Q = 5.57 and 6.26, p = 0.062 and 0.099 for lags 1 and 2, respectively). To address the issue, and to account for any significant autocorrelation in our Brandy Lake data, we included % cyanobacteria biovolume from 14 days before (% $CB_{14db}$) as a possible predictor variable in the forecast models. We also tested the importance of % $CB_{14db}$ for TML.

We developed multivariate regression models for each lake using the predictor variables that were highly cross-correlated with the % CB plus % $CB_{14db}$. The best forecast models were selected through examination of $r^2$, Schwarz Bayesian Information Criterion (BIC), Akaike Information Criterion (AIC) and variance inflation factors (VIFs). AIC assesses the fit and complexity of the models, whereas BIC assesses the fit, complexity and sample size used to develop the model (Johnson and Omland, 2004). To account for any possible non-linear effects of the predictor variables we also assessed the importance of squared and cubed predictor terms such as $TP_{hypo}$. Then to minimize the effects of multicollinearity we removed some of the predictor variables from model development that were significantly correlated, and calculated VIFs to assess multicollinearity effects among the remaining predictor variables (Quinn and Keough, 2002). We used a threshold VIF value of 2.5 as indicative of excessive multicollinearity (Allison, 1999).

We assessed the ability of the selected predictors and the strongest model to forecast % cyanobacteria biovolume by applying a jack-knife approach. For each lake we excluded data for one year and developed forecast models based on only two years data. The two-year models were then used to forecast % cyanobacteria biovolume for the excluded year. We also plotted the observed and predicted values for each omitted year to illustrate the ability of two years of data to predict results for the third year, and to highlight the importance of year-to-year variation in our best models.

## 3. Results

### 3.1. Cyanobacteria dominance

Cyanobacterial dominance (defined herein as >50% cyanobacteria biovolume (Downing et al., 2001)) typically occurred in late summer (August) to early fall (September and October) in BL, but varied in duration and intensity among the three years (Fig 2). Dominance lasted for a longer time period, began earlier (i.e., July), and were more intense (greater dominance) in 2002 and 2003 compared to 2012. In 2002 and 2003 cyanobacteria dominated the algal community accounting for 98–99% (in August and September) of the community, whereas in 2012 they accounted for

**Table 2**
Results for cross-correlations between the time series of % cyanobacteria biovolume and the limnological and meteorological parameters for Brandy Lake and Three Mile Lake. Values represent the correlation *r* values; * and bold indicates significance at $p \le 0.05$.

| Parameter | Brandy Lake | | | Three Mile Lake | | |
|---|---|---|---|---|---|---|
| | No lag (0 day) | Lag 1 (14 day) | Lag 2 (28 day) | No lag (0 day) | Lag 1 (14 day) | Lag 2 (28 day) |
| Stability (S) | 0.2301 | **0.6342*** | **0.6850*** | **0.4917*** | **0.5913*** | **0.5992*** |
| Hypolimnetic $O_2$ | **−0.3867*** | **−0.6087*** | **−0.6871*** | **−0.4991*** | −0.3391 | −0.1837 |
| Secchi depth | **−0.4895*** | **−0.4351*** | −0.2151 | −0.1647 | −0.0149 | 0.1494 |
| Surface temperature | 0.2107 | **0.5481*** | **0.6684*** | **0.5113*** | **0.5206*** | **0.4664*** |
| Volume weighted-TP | **0.466*** | **0.4085*** | 0.2541 | 0.3169 | 0.0818 | −0.1643 |
| Hypolimnetic TN:TP | **−0.3885*** | **−0.6432*** | **−0.6928*** | **−0.4455*** | −0.1616 | 0.0463 |
| Hypolimnetic TP | **0.6235*** | **0.6401*** | **0.4834*** | 0.3206 | −0.1371 | **−0.3969*** |
| 2-d mean wind speed | −0.2503 | −0.1889 | −0.0872 | 0.0876 | 0.2855 | −0.0717 |
| 3-d mean wind speed | −0.3259 | −0.3169 | −0.1877 | −0.0313 | 0.0769 | −0.1893 |
| 5-d mean wind speed | −0.0978 | −0.3202 | −0.1735 | −0.1381 | −0.2020 | −0.3499 |
| 7-d mean wind speed | −0.1983 | **−0.4458*** | **−0.3325*** | −0.3495 | −0.3633 | **−0.4118*** |
| 10-d mean wind speed | **−0.3581*** | **−0.4712*** | −0.2889 | **−0.4235*** | −0.3362 | −0.2939 |
| 2-d mean air pressure | 0.1161 | −0.1212 | −0.1925 | −0.0188 | −0.0953 | 0.1291 |
| 3-d mean air pressure | −0.1756 | 0.225 | 0.2132 | 0.01821 | −0.0846 | 0.1630 |
| 5-d mean air pressure | 0.2256 | 0.2229 | 0.2105 | −0.0173 | −0.1205 | 0.0743 |
| 7-d mean air pressure | 0.2041 | 0.1203 | 0.0003 | 0.1307 | 0.0143 | 0.1284 |
| 10-d mean air pressure | 0.3159 | 0.2051 | 0.1073 | 0.3062 | 0.0605 | 0.0252 |
| 2-d mean air temperature | 0.1342 | **0.4778*** | **0.6294*** | **0.4767*** | **0.5002*** | **0.4686*** |
| 3-d mean air temperature | 0.1063 | **0.4607*** | **0.6216*** | **0.5085*** | **0.543*** | **0.4704*** |
| 5-d mean air temperature | 0.1544 | **0.4941*** | **0.6171*** | **0.5375*** | **0.5541*** | **0.4245*** |
| 7-d mean air temperature | 0.2288 | **0.5303*** | **0.6724*** | **0.5787*** | **0.5837*** | **0.4208*** |
| 10-d mean air temperature | 0.3000 | **0.5571*** | **0.6593*** | **0.5533*** | **0.5895*** | **0.4303*** |
| 2-d total precipitation | −0.0656 | −0.2129 | 0.0267 | 0.2889 | 0.1914 | −0.0490 |
| 3-d total precipitation | −0.1556 | −0.3115 | −0.0607 | 0.0847 | 0.0859 | −0.1297 |
| 5-d total precipitation | −0.0636 | −0.2393 | −0.1531 | 0.0073 | 0.0097 | 0.0499 |
| 7-d total precipitation | 0.0233 | −0.1511 | −0.0912 | −0.0225 | −0.0467 | −0.0196 |
| 10-d total precipitation | 0.0722 | −0.1569 | −0.1599 | 0.0164 | −0.0169 | 0.0772 |

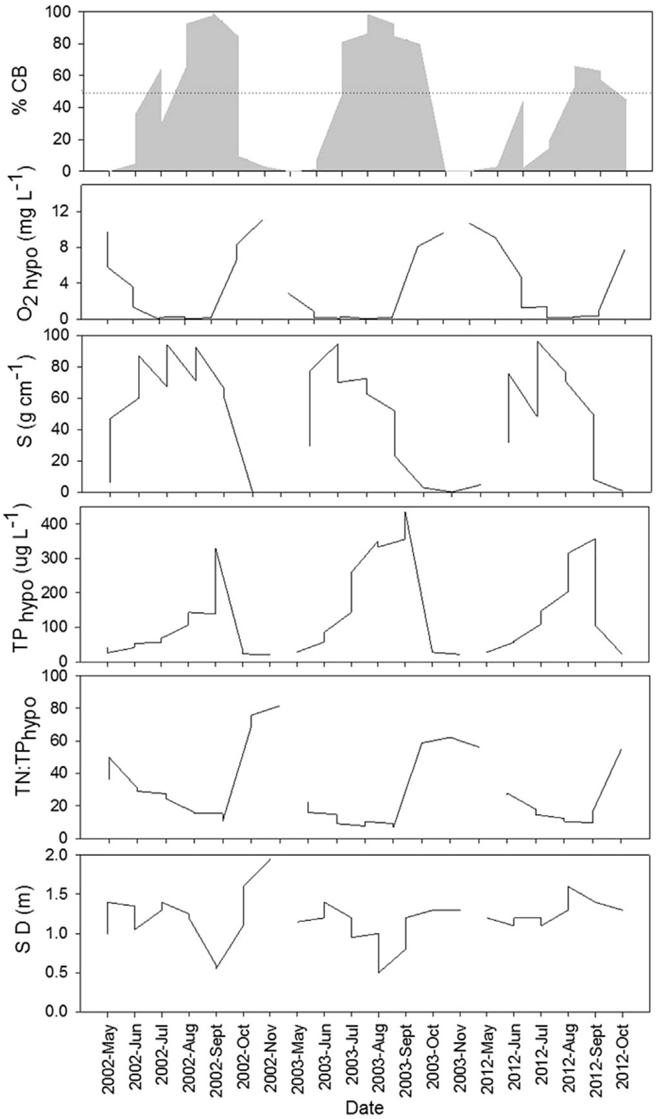


**Fig. 2.** Time series of the algal response variable (% CB = % cyanobacteria biovolume) and predictor variables (S = water column stability, $O_{2hypo}$ = hypolimnetic $O_2$ concentration, $TP_{hypo}$ = hypolimnetic TP concentration and $TN:TP_{hypo}$ = hypolimnetic TN:TP mass ratio, SD = Secchi depth) used for model development for Brandy Lake. The dotted line on the % CB panel indicates the 50% CB threshold used to define dominance.

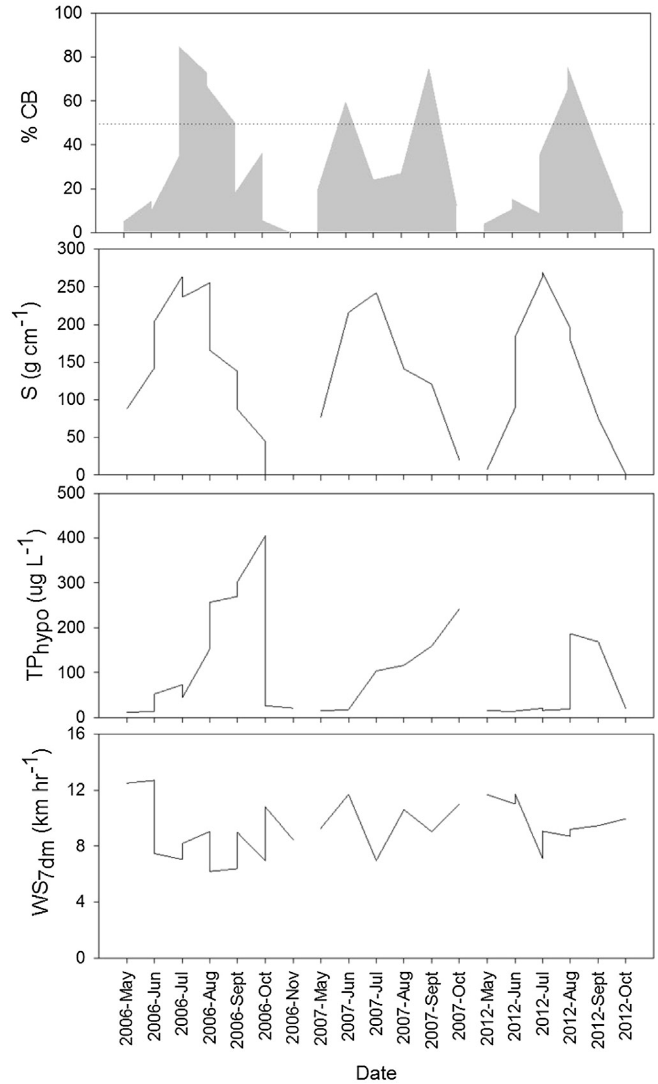


**Fig. 3.** Time series of the algal response variable (% CB = % cyanobacteria biovolume) and important predictor variables (S = water column stability, $TP_{hypo}$ = hypolimnetic TP concentration, and $WS_{7dm}$ = 7-day mean wind speed) used for model development for Hammell's Bay, Three Mile Lake. The dotted line on the % CB panel indicates the 50% CB threshold used to define dominance.

up to 65% (in August) of the algal community.

In TML cyanobacteria dominance varied in duration and intensity among the three years, with the timing of dominance differing from BL (Figs. 2 and 3). In 2007, dominance occurred in June and September, whereas in 2006 dominance occurred between July and September, and in 2012 occurred only in August. Among years, dominance was more intense in 2006 with cyanobacteria accounting for ~85% of the algal community biovolume compared to ~75% in 2007 and 2012, recognizing that peak concentrations are approximations as sampling occurred bi-weekly to monthly.

Cyanobacteria taxonomic composition varied among dominance events, both within and between lakes (Figs. 4 and 5). However, in general, *Aphanizomenon* spp. and *Dolichospermum* spp. were dominant groups in the cyanobacteria community of both lakes. *Dolichospermum* spp. were predominant during the warmest summer months, except in Hammell's Bay in 2006. In contrast, *Aphanizomenon* was a major component of the cyanobacteria community in the spring to early summer and fall. For BL, *Coelosphaerium* spp. and *Oscillatoria* spp. were also important, increasing in relative biovolume in the spring and fall months of some years (Fig 4).

### 3.2. Time series cross-correlations

Time series cross-correlations (Table 2) and Pearson correlations indicated that the important potential predictors of % CB differed between the two study lakes, despite their geographic proximity. For BL, time series analyses indicated that seven and five of the limnological variables were significantly cross-correlated with % CB at a lag 1 (14 days) and lag 2 (28 days) period, respectively (Table 2). Among the meteorological variables, significant cross-correlations were found between % CB and wind speed and air temperature at both 1 and 2 lag periods. For the lag 1 model we used hypolimnetic $O_2$ and TP concentrations, water column stability and Secchi depth as predictors. In contrast, only water column stability and

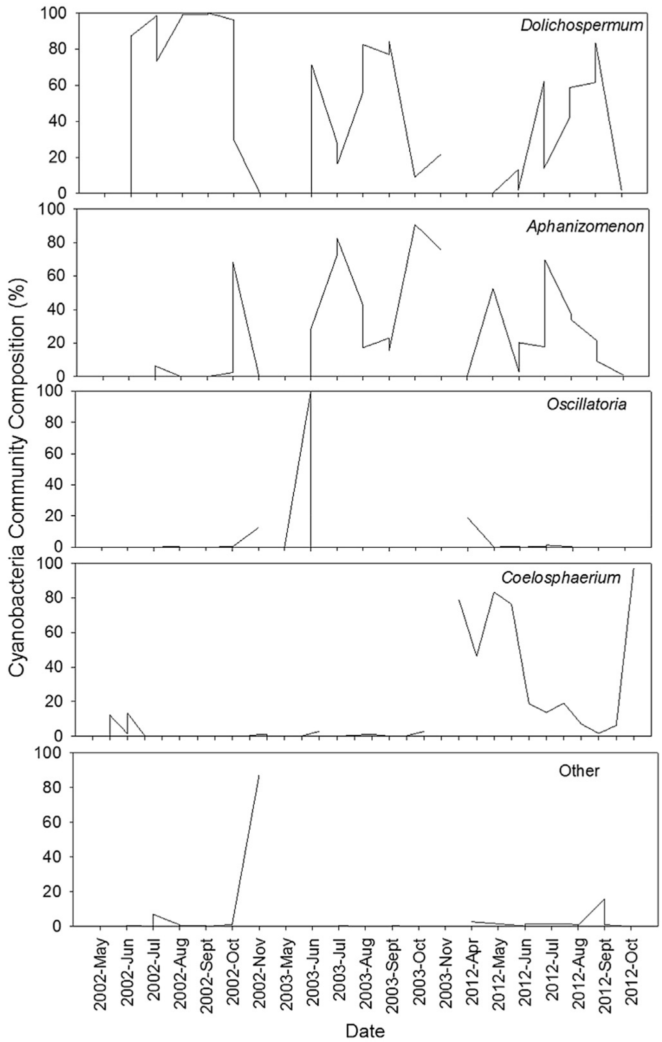


**Fig. 4.** Taxonomic composition of the cyanobacteria community in Brandy Lake. Other taxa included: *Aphanocapsa*, *Aphanotece*, *Chroococcus*, *Merismopedia* and *Romeria*.

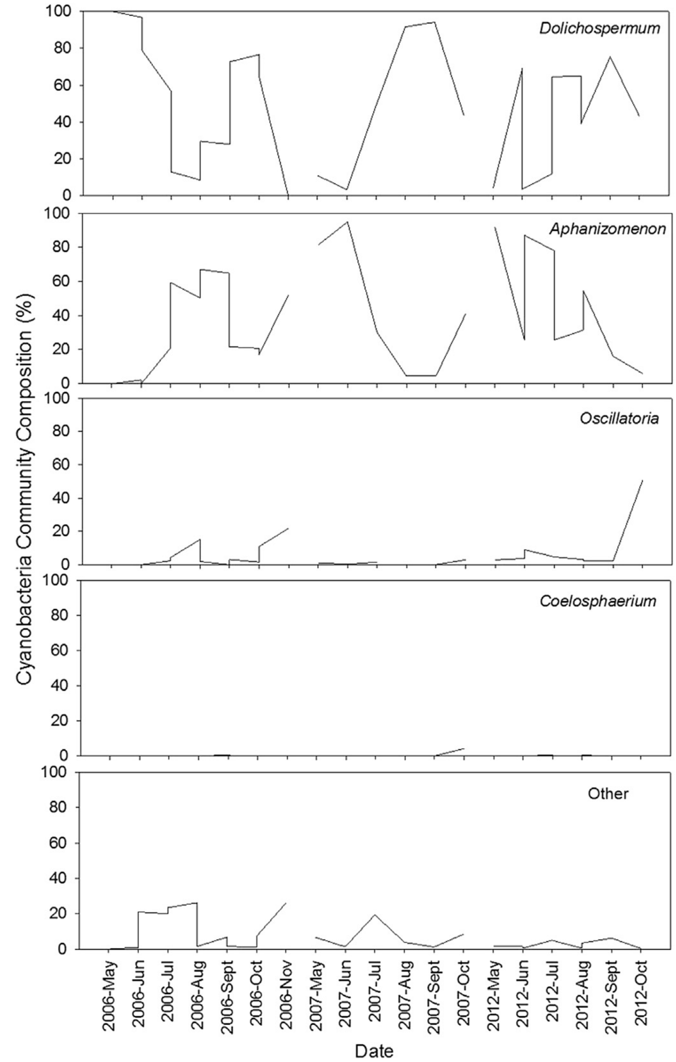


**Fig. 5.** Taxonomic composition of the cyanobacteria community in Hammell's Bay of Three Mile Lake. Other taxa included: *Aphanocapsa*, *Aphanotece*, *Chroococcus*, *Merismopedia*, *Gomphospaeria*, *Nostoc*, *Trichodesmium* and *Lyngbya*.

hypolimnetic $O_2$ and TP were potential predictors for a lag 2 model. Among years, the peaks in cyanobacteria biovolume were negatively correlated to hypolimnetic $O_2$ and positively correlated to hypolimnetic TP concentrations. Additionally, high water column stability and low Secchi depth corresponded to peaks in % CB.

Fewer significant cross-correlations were found for TML compared to BL (Table 2). At a lag 1 period two limnological parameters were significantly cross-correlated with % CB, while three parameters were significantly cross-correlated at the lag 2 period. Among the meteorological variables, a significant cross-correlation was found between % CB and wind speed at the lag 2 period but not at lag 1. In contrast, air temperature was significantly cross-correlated with % CB at both the lag 1 and 2 periods. For the lag 2 model, water column stability, hypolimnetic TP concentration and the 7-d mean wind speed were used as potential predictor variables. In contrast, water column stability was the sole predictor used for the lag 1 model. For TML, peaks in cyanobacteria were generally associated with high water column stability, low hypolimnetic TP concentrations, and low 7-day mean wind speeds. For both BL and TML, models including the other limnological and meteorological parameters are not presented here because they (a) had lower $r^2$, (b) were less parsimonious (higher AICs and BICs) and (c) had high VIFs (>2.5).

### 3.3. Cyanobacteria forecast modelling

For BL, the strongest and most parsimonious multiple regression model for forecasting % CB 14 days in the future (% $CB_{14df}$) included water column stability, hypolimnetic TP and % $CB_{14db}$ (Table 3: % $CB_{14df} = -8.35 + 0.519\ (S) + 0.065\ (TP_{hypo}) + 0.458\ (\%\ CB_{14db})$). While this model is statistically the strongest and most parsimonious model (Table 3: $r^2 = 0.788$; AIC = 269; BIC = 274), it is only marginally different from the model which only includes water column stability and % $CB_{14db}$ as predictors (Table 3: $r^2 = 0.767$; AIC = 270; BIC = 275). VIFs indicate that both of these models have minimal multicollinearity effects among the predictors (Table 3: VIFs ≤ 2.09). Further, the % $CB_{14db}$ was a key predictor for BL cyanobacteria biovolume as it accounted for 8.4%–39.8% of explained variation in the forecast models (Table 3).

For TML, the strongest multiple regression model for forecasting % CB 28 days in the future (% $CB_{28df}$) included water column stability, hypolimnetic TP concentration, and 7-d mean wind speed (Table 3: % $CB_{28df} = 85.8 + 0.164\ (S) - 0.126\ (TP_{hypo}) + 6.96\ (WS_{7dm})$; $r^2 = 0.773$; AIC = 178; BIC = 179). This model is only marginally different from the model that includes water column

**Table 3**
Forecast models for % cyanobacteria biovolume (% CB) in Brandy Lake and Three Mile Lake. The strongest models (highlighted) are those with the highest $r^2$, lowest BIC and AIC and a maximum VIF of <2.5.

| Model | $r^2_{adj}$ | F | Max VIF | AIC | BIC |
|---|---|---|---|---|---|
| **Brandy Lake** | | | | | |
| *Lag 1 (14 day) models (n = 31)* | | | | | |
| % CB = 0.681 + 0.045 ($O_{2hypo}$) + 0.543 (S) − 6.11 (SD) + 0.595 (%$CB_{14db}$) | 0.751 | 23.7 | 3.05 | 276 | 280 |
| % CB = 88.6 − 4.36 ($O_{2hypo}$) + 0.341 (S) − 40.9 (SD) | 0.544 | 12.9 | 2.17 | 293 | 297 |
| % CB = −10.9 + 1.21 ($O_{2hypo}$) + 0.601 (S) − 0.074 ($TP_{hypo}$) + 0.457 (%$CB_{14db}$) | 0.779 | 22.2 | 3.45 | 274 | 279 |
| % CB = −2.30 − 0.144 ($O_{2hypo}$) + 0.552 (S) + 0.156 ($TP_{hypo}$) | 0.667 | 20.9 | 3.18 | 283 | 288 |
| % CB = 0.557 + 0.520 (S) − 6.78 (SD) − 0.066 ($TP_{hypo}$) + 0.431 (%$CB_{14db}$) | 0.783 | 28.1 | 2.47 | 271 | 276 |
| % CB = 27.5 + 0.558 (S) − 24.3 (SD) − 0.141 ($TP_{hypo}$) | 0.699 | 24.3 | 1.19 | 280 | 285 |
| **% CB = −8.35 + 0.519 (S) + 0.065 ($TP_{hypo}$) + 0.458 (%$CB_{14db}$)** | **0.788** | **38.4** | **2.09** | **269** | **274** |
| % CB = −3.37 + 0.158 (S) + 0.562 ($TP_{hypo}$) | 0.678 | 32.6 | 1.06 | 280 | 284 |
| % CB = −8.27 + 0.167 ($O_{2hypo}$) + 0.550 (S) + 0623 (% $CB_{14db}$) | 0.758 | 32.5 | 2.97 | 273 | 278 |
| % CB = 43.8 − 5.05 ($O_{2hypo}$) + 0.323 (S) | 0.461 | 13.8 | 2.12 | 296 | 300 |
| % CB = 1.10 + 0.540 (S) − 6.18 (SD) + 0.594 (% $CB_{14db}$) | 0.761 | 32.8 | 1.35 | 272 | 277 |
| % CB = 66.9 + 0.683 (S) − 46.3 (SD) | 0.477 | 14.7 | 1.01 | 295 | 299 |
| % CB = 13.7 + 0.083 ($TP_{hypo}$) + 0.522 (% $CB_{14db}$) | 0.597 | 23.2 | 2.06 | 287 | 291 |
| % CB = 21.5 − 0.191 ($TP_{hypo}$) | 0.461 | 26.7 | | 294 | 298 |
| % CB = −7.02 + 0.539 (S) − 0.617 (% $CB_{14db}$) | 0.767 | 50.5 | 1.07 | 270 | 275 |
| % CB = 11.1 + 0.725 (S) | 0.369 | 18.6 | | 299 | 303 |
| *Lag 2 (28 day) models (n = 28)* | | | | | |
| % CB = 28.1 − 2.27 ($O_{2hypo}$) + 0.207 (S) − 0.049 ($TP_{hypo}$) + 0.529 (%$CB_{14db}$) | 0.524 | 8.4 | 3.92 | 265 | 269 |
| % CB = 17.0 − 1.19 ($O_{2hypo}$) + 0.344 (S) + 0.406 (%$CB_{14db}$) | 0.530 | 11.2 | 3.16 | 263 | 266 |
| % CB = 9.52 + 0.409 (S) − 0.025 ($TP_{hypo}$) + 0.500 (%$CB_{14db}$) | 0.529 | 11.1 | 3.31 | 263 | 266 |
| % CB = 37.2 − 3.06 ($O_{2hypo}$) + 0.478 (%$CB_{14db}$) | 0.500 | 15.6 | 1.74 | 262 | 265 |
| % CB = 22.7 − 0.049 ($TP_{hypo}$) + 0.776 (%$CB_{14db}$) | 0.482 | 13.6 | 1.88 | 264 | 267 |
| **Three Mile Lake** | | | | | |
| *Lag 1 (14 day) models (n = 24)* | | | | | |
| % CB = 1.82 + 0.171 (S) + 0.207 (%$CB_{14db}$) | 0.349 | 7.17 | 1.17 | 222 | 225 |
| % CB = 5.24 + 0.197 (S) | 0.346 | 12.9 | | 221 | 223 |
| *Lag 2 (28 day) models (n = 21)* | | | | | |
| % CB = 95.3 + 0.184 (S) − 0.133 ($TP_{hypo}$) − 7.59 ($WS_{7dm}$) − 0.161 (%$CB_{14db}$) | 0.778 | 18.5 | 2.38 | 178 | 179 |
| **% CB = 85.8 + 0.164 (S) − 0.126 ($TP_{hypo}$) − 6.96 ($WS_{7dm}$)** | **0.773** | **23.6** | **2.21** | **177** | **178** |
| % CB = −2.30 + 0.269 (S) − 0.042 ($TP_{hypo}$) − 0.042 (%$CB_{14db}$) | 0.620 | 11.9 | 1.47 | 187 | 189 |
| % CB = −2.68 + 0.262 (S) − 0.043 ($TP_{hypo}$) | 0.646 | 18.8 | 1.07 | 183 | 185 |
| % CB = 30.1 − 0.079 ($TP_{hypo}$) + 0.366 (%$CB_{14db}$) | 0.197 | 3.3 | 1.01 | 201 | 203 |
| % CB = 45.5 − 0.088 ($TP_{hypo}$) | 0.102 | 3.2 | | 201 | 203 |
| % CB = 10.1 + 0.262 (S) − 1.85 ($WS_{7dm}$) | 0.645 | 17.7 | 1.14 | 185 | 187 |
| % CB = −9.79 + 0.279 (S) | 0.633 | 34.4 | | 184 | 186 |

Abbreviations are: % CB = % cyanobacteria for a specific lag period; % $CB_{14db}$ = % cyanobacteria biovolume 14 days before, S = water column stability; $O_{2hypo}$ = hypolimnetic oxygen; $TP_{hypo}$ = hypolimnetic total phosphorus; SD = Secchi depth; $WS_{7dm}$ = 7-d mean wind speed.

stability, hypolimnetic TP concentration, 7-d mean wind speed and % $CB_{14db}$ as the predictor variables (Table 3: $r^2 = 0.778$; AIC = 177; BIC = 178). Multicollinearity effects were minimal among the predictor variables for both models (Table 3: VIFs ≤ 2.38).

In general the forecast models over predicted the % CB at low values but under predicted at high values (Fig. 6). However, based on the 50% threshold for cyanobacteria dominance status, the BL and TML models only overestimated the % CB once for each model leading to a false dominance forecast (Fig. 6). For BL, this occurred in July 2002 when the model forecasted 59% CB when the measured value was 29% CB. In contrast, for TML this occurred in September 2012 when the model forecasted 50% CB while the measured biovolume was only 41%. Additionally, the BL model substantially underestimated % CB in June 2012 when the model forecasted 5% CB while the measured value was 44%.

Jackknifing for both Brandy Lake and Three Mile Lake indicated that models generated with only two years of data were generally good at forecasting the cyanobacteria relative biovolume and dominance (Table 4 & Fig. 7). For TML there was only one occasion in 2006 where the model based on 2007 and 2012 data forecasted low % CB that did not reflect cyanobacteria dominance. In contrast, for BL there were three occasions in 2002 where the 2003 and 2012 model forecasted % CB values that did not reflect cyanobacteria dominance.

## 4. Discussion

### 4.1. Forecast models

The importance of water column stability and nutrients in the forecast models suggest that cyanobacteria dominance is affected by both nutrient and temperature thresholds, plus any indirect interactive effects from internal nutrient loading (Huber et al., 2012; Rigosi et al., 2014; Taranu et al., 2012). Warm temperatures that enhance stratification promote cyanobacteria dominance because buoyant cyanobacteria species are able to take advantage of high hypolimnetic nutrient concentrations that indirectly result from stratification and associated oxygen depletion in bottom waters (Huber et al., 2012; Rigosi et al., 2014; Wagner and Adrian, 2009). Wagner and Adrian (2009) indicated that blooms were favoured when high temperatures lead to extended periods of water column stability in lakes with elevated TP concentrations. Additionally, Taranu et al. (2012) reported that the effect of elevated temperature on cyanobacteria growth and abundance were intensified by higher nutrient concentrations. Furthermore, cyanobacteria growth is directly affected by temperature and indirectly dependent on critical nutrient loadings, which are generally lower at higher temperatures because increased mineralization at higher temperatures leads to higher nutrient availability (Mooij et al., 2007).

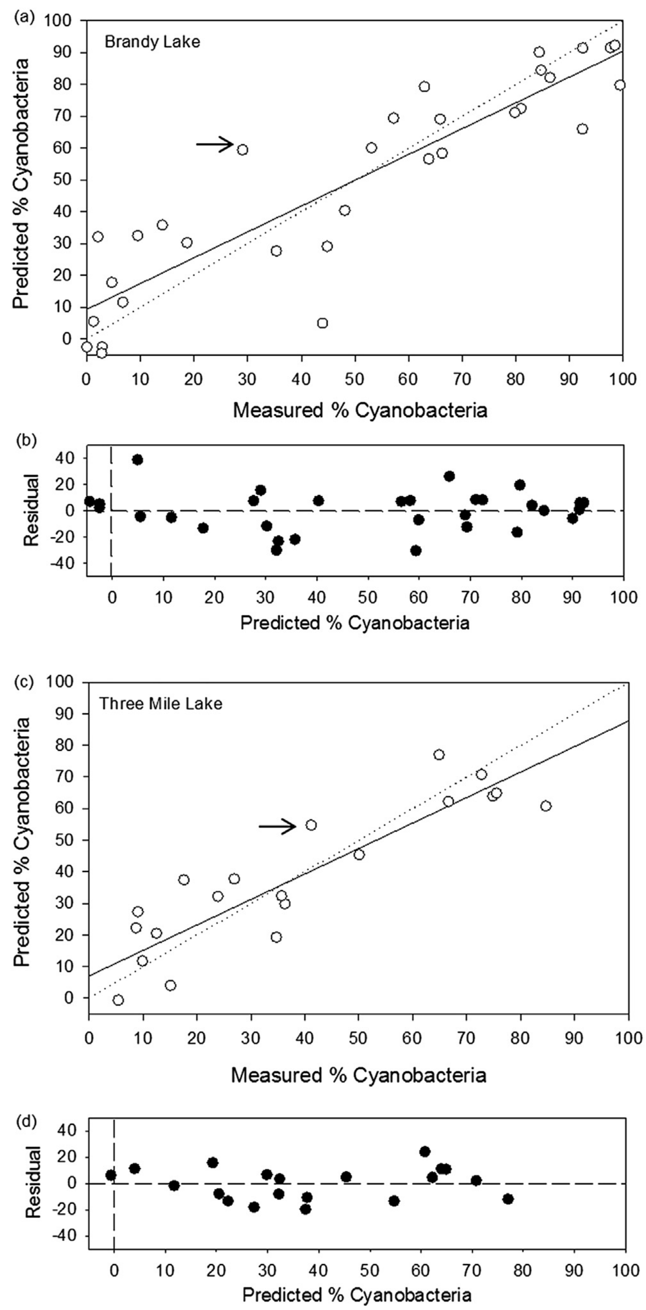


**Fig. 6.** Regression and residual plots of the measured versus predicted % cyanobacteria biovolume for (a) Brandy Lake (using model: % $CB_{14df} = -8.35 + 0.519(S) + 0.065(TP_{hypo}) + 0.458(\% CB_{14db})$), (b) Brandy Lake predicted residuals, (c) Hammell's Bay of Three Mile Lake (% $CB_{28df} = 85.8 + 0.164(S) - 0.126(TP_{hypo}) - 6.96(WS_{7dm})$) and (d) Hammell's Bay predicted residuals. The solid lines on plots (a) and (c) represent the best-fit linear regressions (BL: Predicted % CB = 9.37 + 0.810(Measured % CB), $r^2_{adj} = 0.804$, $p < 0.001$; TML: Predicted % CB = 7.07 + 0.806(Measured % CB), $r^2_{adj} = 0.796$, $p < 0.001$) and the dotted lines indicate the 1:1 line. Arrows indicate when the measured % cyanobacteria values were significantly overestimated by the best-fit models.

Water column stability is a key predictor of % CB in both of the study lakes. At the lake level, thermal stability is likely a better indicator of percent cyanobacteria than air temperature alone because it incorporates the interactive effects of temperature, lake morphometry, and other factors including water colour. Warm surface temperatures increase water column stability by maintaining the density differences between cool hypolimnetic and warm surface waters. Reduced wind speeds also promote water column stability by reducing turbulent mixing within the water column. While stratification is not always affected by increased air temperature (Elliot et al., 2005), in our lakes we found significant correlations between these two parameters (Pearson correlations: $r > 0.689$, $p < 0.0001$). Wagner and Adrian (2009) reported that thermal stability above 44 g $cm^{-1}$ for more than 3 weeks favoured cyanobacteria bloom formation in Lake Müggelsee, a lake which is similar to BL in lake depth. In agreement with Wagner and Adrian (2009) we found that in BL, as thermal stability above 44 g $cm^{-1}$ persisted throughout the summer months, so too did cyanobacteria dominance.

Despite the inclusion of similar predictor variables (water column stability and nutrients), the models for forecasting cyanobacteria biovolume and potential bloom occurrence in BL and TML were different in several ways. Firstly, the lag period of the strongest forecast model differed for the two lakes. The 14 day forecast models (lag 1) were stronger for BL, whereas the 28 day models (lag 2) were stronger for TML. Secondly, the best TML model consists of both limnological and meteorological variables, whereas the best BL model is based solely on limnological parameters. Three factors that may have contributed to differences in the models developed for BL and TML are: nutrient concentrations, water transparency and lake morphometry. Brandy Lake had a higher TP concentration, and larger drainage ratio compared to TML. Hammell's Bay of TML is deeper and has a larger surface area than BL, more transparent (i.e., of lower dissolved organic carbon concentration), and connected to a shallow main basin with which water exchange may occur. A deeper water column, larger hypolimnetic volume, and higher transparency in Hammell's Bay means that it takes longer for (1) the water column to warm up and stratification to stabilize, (2) anoxic conditions to develop in the hypolimnion, and (3) internal phosphorus loading to commence under anoxic conditions deep in the water column. The larger surface area of TML compared to BL also translates to a greater influence of wind on water column stability (Read et al., 2012); thereby explaining the inclusion of wind speed in the TML model but not in the BL model. Additionally, it is possible that flushing rate, an important factor which has been linked to cyanobacteria bloom formation (Elliot, 2010, 2012), plays a role in the cyanobacteria dynamics within the two lakes as TML has a longer flushing rate compared to BL (long-term mean = 6.75 yr and 2.79 yr, respectively), and thus impacts the lake response time to dominance events. Together these factors may explain why a 28 day forecast model was more suitable for TML, whereas a 14 day model was appropriate for shallower BL.

**Table 4**
Forecast models for Brandy Lake and Three Mile Lake that are based on two years data. The predictors of the strongest models in Table 3 were used to develop all models.

| Lake | Years | Model | $r^2_{adj}$ | p-value |
|---|---|---|---|---|
| Brandy *(Lag1, 14 day)* | 2002 & 2003 | $\% CB = -15.1 + 0.675(S) + 0.098(TP_{hypo}) + 0.365(\%CB_{14db})$ | 0.894 | <0.0001 |
| | 2002 & 2012 | $\% CB = -6.46 + 0.513(S) + 0.038(TP_{hypo}) + 0.464(\%CB_{14db})$ | 0.674 | <0.0001 |
| | 2003 & 2012 | $\% CB = 8.14 + 0.104(S) + 0.033(TP_{hypo}) + 0.676(\%CB_{14db})$ | 0.862 | <0.0001 |
| Three Mile *(Lag 2, 28 day)* | 2006 & 2007 | $\% CB = 91.2 + 0.178 (S) - 0.131 (TP_{hypo}) - 7.49 (WS_{7dm})$ | 0.794 | 0.0003 |
| | 2006 & 2012 | $\% CB = 78.2 + 0.162 (S) - 0.124 (TP_{hypo}) - 6.02 (WS_{7dm})$ | 0.761 | <0.0001 |
| | 2007 & 2012 | $\% CB = 84.7 + 0.166 (S) - 0.169 (TP_{hypo}) - 7.12 (WS_{7dm})$ | 0.743 | 0.0053 |

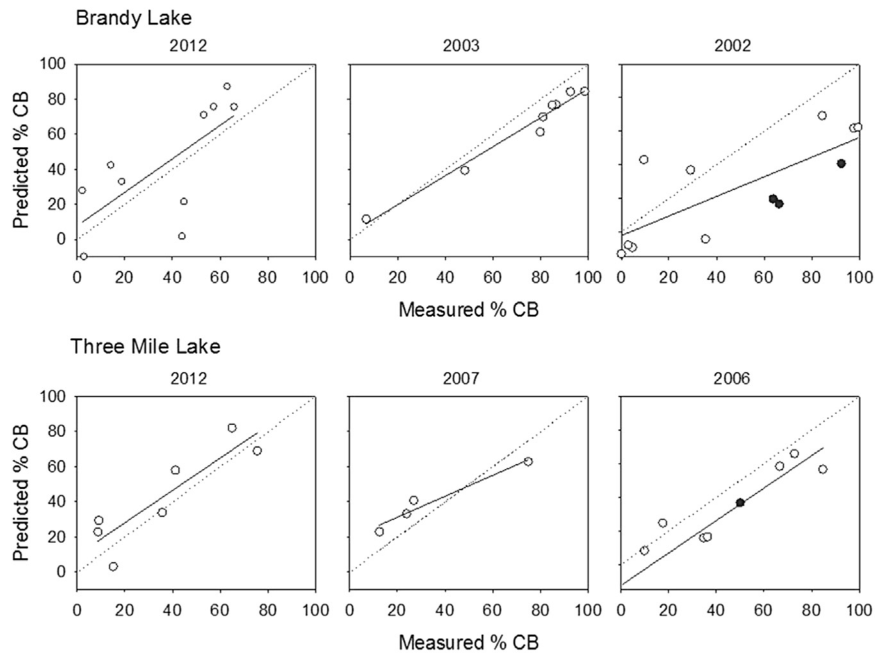


**Fig. 7.** Measured % Cyanobacteria biovolume (Measured %CB) for single years versus % Cyanobacteria biovolume predicted (Predicted % CB) using the two year forecast models presented in Table 4 for Brandy Lake and Hammell's Bay of Three Mile Lake. Measured % CB values which were under predicted by the two year models and therefore did not reflect dominance are highlighted.

## *4.2. Other considerations*

In addition to the factors considered here, other factors can also influence cyanobacteria dominance in lakes. For example, it is possible that iron availability ($Fe^{2+}$) was also a driving factor for cyanobacteria dominance since they have been found to have a high $Fe^{2+}$ requirement that can result in $Fe^{2+}$ limitation when supply is low (Molot et al., 2010). Further, $Fe^{2+}$ can also be indirectly linked to cyanobacteria through the coupling of phosphorus release from sediments (Loh et al., 2013). We were unable to directly assess the importance of iron because $Fe^{2+}$ availability data were unavailable for the study lakes. However, we did consider hypolimnetic $O_2$ concentration, a parameter that is closely linked to $Fe^{2+}$ availability, for the cross-correlations and model development. Cyanobacteria demand for high $Fe^{2+}$ concentration can only be satisfied if anoxia develops in the hypolimnion, thereby resulting in internal $Fe^{2+}$ loading from sediments and prevention of $Fe^{2+}$oxidation to $Fe^{3+}$ (Molot et al., 2014). We were therefore able to indirectly address the importance of this mechanism by using oxygen concentration as a potential predictor variable in our models.

In general, the models performed well to forecast cyanobacteria dominance using the 50% threshold, as it only falsely forecasted dominance once for each model. For BL the model overestimated % CB in the early summer of 2002 during a period of relatively low % CB between a spring and extensive summer blooms. For TML, the forecast model over predicted % CB in early fall 2012 shortly after a distinct bloom in August that year. In both cases the data indicated that conditions were appropriate for a high percentage of cyanobacteria biovolume and thus dominance (stable water column, low wind speed, etc.), but dissipation occurred for reasons we cannot account for in this study. In addition to over prediction for BL, in late spring (June) of 2012 the BL model under predicted % CB on one occasion. The model forecast prediction was low because the preceding water column stability was only 31 g $cm^{-1}$ (surface water temperature was below 20 °C) and $TP_{hypo}$ was 57 µg $L^{-1}$. It is unclear how cyanobacteria became dominant under such conditions.

We believe that it is unlikely that the use of data from different years for the two lakes have affected the outcome of our forecast modelling for the following reasons. While inter-annual differences in meteorological parameters may have occurred during the data collection period, it appears that those differences are less important compared to the chemical and physical differences between the lakes. For 2012, the one year of this study that both lakes were sampled, it is clear that the two lakes are chemically and physically different (Figs. 2 and 3). These differences combined with the dissimilar morphometries of BL and Hammell's Bay of TML translated to differences in lake response times, and inevitably, the forecast models. Furthermore, the jackknifing results illustrate that importance of the predictor variables selected for the forecast models was not affected by year to year differences.

## 5. Conclusion

From a management perspective, the ability to forecast cyanobacteria dominance is invaluable to land managers as monitoring and assessment tools, and the public, as a means to assess safety and potential exposure to cyanobacteria. Development and application of lake-specific forecast models require careful data collection over several years. Data collection should focus on as many chemical, physical and morphometric parameters as possible, but our analyses indicated that temperature profiles and nutrient chemistry parameters are particularly important. Sampling frequency should be biweekly at minimum, although weekly collection will likely improve accuracy.

Predicting and forecasting the occurrence of cyanobacteria dominance in lakes across the landscape can be a challenging task. Broad scale spatial studies (e.g. Beaulieu et al. (2013) and Taranu et al. (2012)) are useful, albeit at a lower confidence level, for deciphering the predictive factors (nutrients and climate) for cyanobacteria blooms across the landscape. The results presented here echo previous studies indicating that nutrients and climate driven limnological factors, in particular water column stability, are key drivers of cyanobacteria dominance at the lake scale. Our results also illustrate, however, that insightful models for lake management can be developed to forecast cyanobacteria dominance at the lake-level, and these may be required to forecast cyanobacteria dominance with greater confidence within lakes. Furthermore, our findings have implications for studies done at a much broader scale as it illustrates that even though the two study lakes are in close proximity of each other, the forecast models are quite different as the lakes differ dramatically in morphometric, physical and chemical characteristics. Variability in these characteristics is an important source of variation in broad, landscape models that affects their predictive power. We recommend that future work should take these factors into consideration when exploring and assessing the variability in cyanobacteria dominance at the both the lake and landscape levels. Future scenarios of global and regional change indicate that some of the key drivers (water column stability and nutrients) are expected to change as land use changes and global warming continues, hence they will impact cyanobacteria dynamics in temperate lakes.

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