

Interpolating and forecasting lake characteristics using long-term monitoring data

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Abstract

It is virtually impossible to quantify the limnological characteristics of every aquatic ecosystem all the time. The goal of this study was to assess the capacity of lake-monitoring data to predict annually resolved characteristics in systems where measurements are not always made. To address this, we provide an analysis of interpolation (i.e., predicting a current lake characteristic based on current characteristics of other lakes) and forecasting (i.e., predicting a current lake characteristic based on historical trends and characteristics of a set of study lakes) in seven lakes over a 28-yr time frame. The most effective interpolations are generated using 12–15 yr of training data. Interpolation models are 29% more effective, on average, when historical trends (forecasting) are also incorporated into the models. Forecasting models that predict lake characteristics using long-term trends in the focal lake were improved by including historical observations from other lakes. Direct comparisons of different prediction models further demonstrated that it is sometimes more effective to generate predictions based on a set of previously measured conditions (forecasts) rather than a set of known regional conditions that have been recently quantified (interpolations). Basic monitoring data have the potential to be upscaled to generate predictions of lake characteristics, but the effectiveness of predictions depend on the training data characteristics and prediction approaches employed.

If one cannot directly measure a characteristic of an aquatic ecosystem, how can one best estimate it? A goal of many aquatic studies is to determine ecosystem characteristics without having to measure them everywhere and all the time (Fee and Hecky 1992; Downing et al. 2001; Pace 2001). As with many disciplines, there is a long history of predicting ecosystem characteristics in the aquatic sciences (Peters 1986; Likens 1989; Cole et al. 1991). Predictions in lakes, for example, have been generated using models that range in complexity from simple relationships between phosphorus and chlorophyll (Dillon and Rigler 1974) to complex efforts that couple terrestrial and aquatic process models, hydrologic and landscape models, and climate (Cardille et al. 2007). Lake prediction models are often driven by information about the system's watershed (Soranno et al. 1996; Fraterrigo and Downing 2008), attributes of the lake (Vollenweider 1969), and/or processes occurring within the system (Ahlgren et al. 1988) that are often not readily available for every lake of interest (Evans et al. 2010).

A clear need exists to develop novel predictive approaches that help increase scientific understanding and management of aquatic ecosystems (Pace 2001). Complex models are not necessarily synonymous with the best predictions, and simple models can be effective for generating predictions in a diverse range of situations (Downing et al. 2001; Debra et al. 2004). Research and management programs often collect baseline-monitoring data in aquatic systems, and upscaling this monitoring data to regional spatial scales has the potential to be a simple, effective approach for generating predictions through space and time. Two basic approaches are interpolation and forecasting prediction models. Interpolation models generate predictions based on a known set of known current conditions, while forecasting models generate predictions

using past or historical conditions without knowledge of any current states. When lake dynamics are strongly correlated to regional scale drivers, suites of lakes often respond in a similar manner due to shared drivers among the systems (Baines et al. 2000; Magnuson et al. 2006c; Vogt et al. 2011). Consequently, information from monitored lakes can be used to interpolate the state of systems where measurements cannot be made (i.e., predict the current state of a focal system using observations of the current state in other systems; Evans et al. 2010). While interpolated predictions such as these can be generated with very little training data (Evans et al. 2010), synchrony among systems may not always be evident without many years of data (Magnuson et al. 2004). Thus, interpolation accuracy may vary depending on the extent of training data, and it is unclear how much training data is needed to maximize the effectiveness of simple interpolation models. Answers to these and related questions could improve methods for upscaling baseline-monitoring data to the wider landscape.

The upscaling of baseline-monitoring data to the wider landscape using simple interpolation models has some potential limitations that may need to be considered as well. Interpolation models based on observations of current conditions in monitored systems lack any historical context (Magnuson 1990) in both the monitored systems and the focal systems where predictions are being generated. The lack of historical context emerges on two fronts. First, aquatic ecosystems often have memory (i.e., they are influenced by past events) and that memory can have important effects on current and future dynamics within the focal system (Montgomery and Reckhow 1984). Omission of memory or historical effects in interpolation models could therefore limit prediction capacity in these models. Historical states of the lakes used to generate interpolations may be important as well. Time lags are common in ecological systems (Magnuson 1990) and if

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different lakes respond to large-scale changes in similar ways at different time frequencies, individual lakes may help forecast (i.e., predict future state using only historical observations) how other lakes will change in the future. Scenarios could arise where the best predictor is not the current state of a nearby system, but rather the state of that system at a prior time. Thus, although it is clear that historical context can be important, the extent to which interpolation models could be biased by excluding this type of information is not apparent.

Finally, although interpolation models rely on synchrony among systems to generate predictions, limnological variables do not always vary in a similar fashion among lakes, even adjacent ones (Kratz et al. 1998). In lakes, physical variables influenced by variation in climate are more coherent than are chemical variables, which are, in turn, more coherent than biological variables (Kratz et al. 1998; Baines et al. 2000; George et al. 2000). This pattern generally reflects the relative importance of external vs. within-lake drivers of limnological variates (Vogt et al. 2011). As a result, interpolation might be less effective for generating predictions for variables or systems that are not characterized by strong synchrony with neighboring aquatic ecosystems (Evans et al. 2010). However, if systems have memory or predictable cycles (Sanderson 1998; Sanderson et al. 1999; Beisner et al. 2003), it might be possible to still use historical monitoring data to forecast present conditions (Anderson 1995; Ives 1995). On the other hand, generating predictions based on unknown future conditions might still be less effective than using a set of known regional conditions that have already been measured, even if those predictions are imprecise. Consequently, there is still much to be learned about the relative effectiveness of interpolation vs. forecasting models and the situations where forecasting models might be more effective than interpolation models.

While capacity of simple monitoring data to generate predictions at regional spatial scales is evident (Baines et al. 2000; Evans et al. 2010), there is still a lot to be learned about how to most effectively upscale this type of data to the broader landscape. The utility of predictions involves both measuring model capabilities and comparisons of alternate approaches (Peters 1986). We use 28 yr of data collected in seven lakes as part of the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program to assess basic questions about temporal and spatial predictions of lake characteristics using monitoring data. The extensive spatial and temporal characteristics of this dataset provides a unique opportunity to address how much data is needed to interpolate lake characteristics, the importance of incorporating historical context when generating predictions, and the relative effectiveness of interpolation and forecasting models across a range of variables and lakes.

Methods

Study site and data—Chemical, physical, and biological data were collected as part of the NTL-LTER program from seven lakes located in the Northern Highlands Lake

District of Wisconsin (Fig. 1). Lakes in this region are characterized by moderate to low acid-neutralizing capacity, conductivity, and productivity (Hanson et al. 2007). All study lakes are located within the Trout Lake (TR) watershed and hydrologically linked via groundwater and/or surface water (Webster et al. 2006). Crystal Lake (CB; 0.005 km²) and Trout Bog (TB; 0.011 km²) are both small highly colored dystrophic lakes. Crystal Lake (CR; 0.37 km²), Big Muskellunge Lake (BM; 3.96 km²), and Sparkling Lake (SP; 0.64 km²) are clear lakes with no surface-water inputs while Allequash Lake (AL; 1.68 km²) and Trout Lake (TR; 16.08 km²) both have surface-water inputs and outputs. The region and focal lakes have been studied extensively for > 2 decades as part of the NTL-LTER program, and much of what is known about lakes situated in this landscape is summarized by Magnuson et al. (2006a).

To address our research questions, several physical, chemical, and biological variables were extracted from NTL-LTER datasets (<http://lter.limnology.wisc.edu>; Table 1). Dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total nitrogen (TN), and total phosphorus (TP) were selected because they are important components of carbon and nutrient budgets of lakes. Three variables were selected due to their direct or indirect links to climate. Calcium (Ca) concentrations are influenced by drought and are an indicator of groundwater inputs to lakes (Webster et al. 2000; Lottig et al. 2011). Long-term trends in sulfate concentrations (SO₄) have been strongly influenced by reductions in emissions, while inter-annual variability is related to climate (Webster et al. 2006). Epilimnetic depth (Epi) was selected as a variable influenced by physical dynamics, including climate (Robertson and Ragotzkie 1990). Finally, chlorophyll *a* (Chl *a*) concentrations were selected as a limnological variable responsive to grazing as well as nutrient supply (Sanderson et al. 1999).

The NTL-LTER program measured these variables at various time intervals. Ca and SO₄ were collected quarterly, while the remaining variables were collected on at least a monthly basis, but no more than 20 times yr⁻¹. We used epilimnetic data from all sampling periods except for Chl *a* and Epi (Table 1). We used Chl *a* samples collected from the epilimnion during the stable stratified summer period of July and August and Epi measures during August when Epi is typically at its maximum. Individual samples were checked for outliers by removing observations that were > 2.5 standard deviations from the annual mean. Outliers were generally high values measured at the bottom of the epilimnion, dilute samples collected at the surface during ice cover, or transcription errors in the database. All variables were checked for approximate normality using probability plots and, if necessary, were transformed to better approximate the normal distribution (Table 1). We used annually resolved values for the analyses reported here.

Data analysis—We used four different statistical models to assess predictions based on comparative (interpolation) and long-term historical (forecasting) data. In this paper, a focal lake is the lake for which we are making predictions,

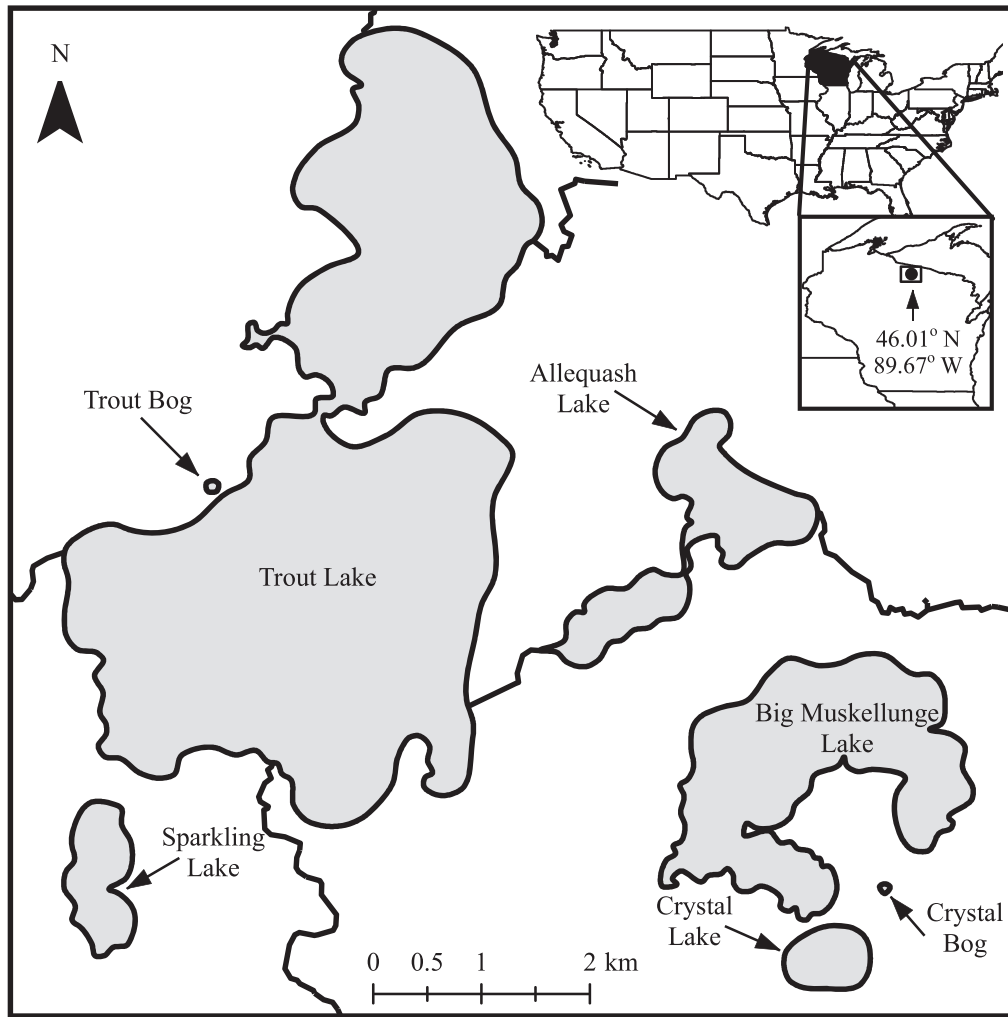


Fig. 1. Site location map of the seven study lakes from the North Temperate Lakes Long-term Ecological Research (NTL-LTER) site. Crystal Lake (CR), Crystal Bog (CB), and Big Muskellunge Lake (BM) are linked to Allequash Lake (AL) via groundwater flow. AL is directly connected to Trout Lake (TR) via Allequash Creek. Sparkling Lake (SP) and Trout Bog (TB) are linked to TR via groundwater flow. CR and CB are located at the highest elevation (502 m) in the landscape and TR at the lowest (492 m).

Table 1. Summary of variables used in predictive models. Sample frequency denotes the frequency used to calculate annual means, not necessarily the frequency at which samples were collected from each lake. Ca = calcium, TN = total nitrogen, DOC = dissolved organic carbon, DIC = dissolved inorganic carbon, SO₄ = sulfate, TP = total phosphorus, Epi = epilimnetic depth, Chl *a* = chlorophyll *a*.

| Variable | Sample period | Sample frequency | Transformation |
|---------------------------------------|---------------|------------------|----------------|
| Ca (mg L ⁻¹) | 1982–2007 | quarterly | natural log |
| TN (mg L ⁻¹) | 1986–2007 | monthly | natural log |
| DOC (mg L ⁻¹) | 1986–2007 | monthly | natural log |
| DIC (mg L ⁻¹) | 1986–2007 | monthly | none |
| SO ₄ (mg L ⁻¹) | 1982–2007 | quarterly | none |
| TP (mg L ⁻¹) | 1986–2007 | monthly | natural log |
| Epi depth (m) | 1981–2008 | annually | none |
| Chl <i>a</i> (mg L ⁻¹) | 1981–2007 | biannually | natural log |

and neighboring lakes are lakes located within the same watershed. Models were compared on the basis of their in-sample prediction errors. We also computed a rarefaction analysis (described below) in which we use out-of-sample prediction errors. Models with a high capacity to predict a given lake variable should exhibit small prediction errors. Prediction capacity of each model was calculated as the standard deviation of prediction errors divided by the long-term average of the limnological variable being predicted in the focal lake. This measure of model performance is unitless and normalized for differences in scale. As a result, it is useful for comparing a diverse set of variables and lakes. Thus, among all variables, the model or variable with the lowest prediction capacity was predicted with the greatest precision. We assessed the changes in prediction capacity between individual models as percent difference.

The first (Eq. 1) and most basic prediction approach (Comparative [C]) interpolates current (year *t*) limnological characteristics in a focal lake ($y_{L,t}$) based on the current characteristics of neighboring lakes ($x_{Li,t}$):

$$y_{L,t} = f(x_{L,t}) + \varepsilon_t \quad (1)$$

Multiple linear regression (MLR) and Akaike's information criterion (AIC) were used to select the combination of neighboring lakes that was the best overall predictor (lowest AIC value) using a backward selection process and the [R] Statistics Package. Time is not explicit in this interpolation model and data used to generate predictions using this model do not need to be continuous.

Using the basic interpolation C model, we first ask how long (year) a training dataset needs to be before interpolation capacity is maximized and whether the composition of the training datasets (i.e., which years are used to generate the interpolations) matters. In order to answer this question, we compared interpolation capacities of models as a function of how many years of data are included in the training dataset. Because research programs may not have access to data collected in consecutive years, model performance was calculated using training datasets composed of different combinations of 'observed' years to determine whether prediction capacity was sensitive to composition of the training dataset (e.g., yr 1, 2, 5, 11, 13 vs. yr 3, 12, 16, 19, 22 in a 22-yr record). If the combination of years included in the training dataset were important, variance among different potential training datasets of a given length would be expected to be large. On the other hand, if the composition of the training dataset matters little, we would expect a similar overall prediction capacity regardless of which specific years were used in the training dataset. Thus, this rarefaction analysis provides two pieces of information: how prediction capacity changes as a function of the number of years included in the training dataset, and the sensitivity of the model to the specific observations (year) used to build the interpolation model.

Our analyses start with a minimum of 8 yr (statistical requirement due to the number of neighboring lakes in the dataset) and extend through the length of record (22–28 yr). For each group of analyses (i.e., training-dataset length), we determine the maximum number of potential training datasets (i.e., unique year combinations) given the desired training-dataset length where n equals the dataset length and k equals the training-dataset length.

$$\text{No. potential training datasets} = \frac{n!}{k!(n-k)!} \quad (2)$$

When the number of combinations exceeded 100 for a given training-dataset length, we randomly choose 100 different potential training datasets, and, in all other cases, used every combination (e.g., for a 28-yr record, there is only one potential training dataset that includes all 28 observations). Using DOC as an example, this approach resulted in 100 unique 8, 10, 12, 15, 20-yr-long datasets, and a final training dataset using all 22 yr of data (total 501 training datasets).

In a given focal lake (seven total) and for each potential training dataset, we determined the set of neighboring lakes most capable of interpolating the focal lake's state using MLR and AIC as outlined above for the C model. Estimated parameters from the resulting C model were extracted and used to interpolate a focal lake's state over

the entire record of observations (e.g., a 28-yr record interpolated from parameters estimated using an 8-yr training dataset). Prediction capacity was estimated for two different validation datasets. Prediction capacity was quantified using data from the entire record and prediction errors represent a mix of both in- and out-of-sample errors. Prediction capacity was also estimated using only observations that were not part of the training dataset (out-of-sample errors only). In the second case, as training datasets get longer, out-of-sample validation datasets become shorter (e.g., for a 22-yr record, a 20-yr training dataset results in a 2-yr validation dataset). Due to the potential difficulties of estimating model performance based on very short validation datasets, we constrained our analysis to out-of-sample validation datasets with a minimum length of 7 yr. We quantified the sensitivity of the results to the composition of the training dataset based on prediction capacity standard deviation among training datasets of the same length. This overall process was completed for each of the eight variables examined in this study and, for each variable, we report the average values based on the interpolation results in all seven lakes.

Next, we assessed the importance of accounting for historical context in basic interpolation C models using an Enhanced Comparative (EC) approach. The EC models included the prior year's ($t - 1$) state of neighboring lakes ($x_{L,i,t-1}$) and the focal lake ($y_{L,t-1}$) in addition to the current (t) characteristics of neighboring lakes ($x_{L,i,t}$),

$$y_{L,t} = f(x_{L,i,t}, x_{L,i,t-1}, y_{L,t-1}) + \varepsilon_t \quad (3)$$

The structure is similar to the C model, where $y_{L,t}$ is predicted by $f(\dots)$, which is a linear function of the parameters, but the EC model includes the additional forecasting parameters $y_{L,t-1}$ and $x_{L,i,t-1}$ (Eq. 3). Although time is not explicit and continuous data are not essential in the C models, including forecasting parameters in the EC models necessitates acquiring continuous monitoring data to generate these mixed forecasting and interpolation predictions. Additionally, because EC models include the same parameters as the C models, EC models cannot perform worse than C models (e.g., if forecasting parameters are nonsignificant, the EC model is essentially a C model). The best set of predictors was determined using the same procedure as previously described in the C approach. We interpret changes in the model composition and/or prediction capacity as a measure of the ability of lakes to serve as sentinels of future change. If the forecasting parameters in this model are not selected with AIC, prediction capacity will not change relative to the C model and it indicates that forecasting parameters (historical context) do not increase the prediction capacity of the interpolation models. On the other hand, if forecasting parameters are selected, the change in model composition and prediction capacity demonstrate the increased ability of mixed interpolation and forecasting models to predict annual lake dynamics.

To assess the relative utility of predictions generated using known current conditions (interpolations; C models) or historical trends (forecasting), we quantified the ability

of historical long-term monitoring data to forecast future unknown conditions in lakes using two pure forecasting approaches. First, a simple temporal forecasting model (T) predicted a focal-lake characteristic ($y_{L,t}$) as a function of the historical time series ($y_{L,t-j}$) of the focal lake using an autoregressive (AR) time series (TS) model where $f(\dots)$ is a linear combination of AR terms.

$$y_{L,t} = f(y_{L,t-j}) + \varepsilon_t \quad (4)$$

We did not de-trend any TS of lake characteristics because TS were too short (22–28 observations) for detailed autocorrelation analysis (Chatfield 1980). Due to the short TS length we also limited time lags to a maximum of 4 yr. For each variable–lake combination we checked the TS for significant serial correlation using autocorrelation and partial autocorrelation functions (ACF and PACF, respectively) in the [R] Statistics Package. The most significant time lag was incorporated into the TS model and the resulting residuals were checked again for significant time lags; the process was repeated until no significant time lags existed.

The second forecasting approach (Enhanced Temporal [ET]) assessed how much additional predictive power could be obtained in basic T models by including historical trends in neighboring systems. Equation 5 forecasts the focal lake's current characteristics ($y_{L,t}$) from historical characteristics in the focal lake ($y_{L,t-j}$) and prior year's ($t - 1$) values in neighboring lakes ($x_{Li,t-1}$). Current focal-lake characteristics are thus forecasted by a linear combination of two separate types of historical terms for the focal lake and neighboring lakes:

$$y_{L,t} = f(y_{L,t-j}, x_{Li,t-1}) + \varepsilon_t \quad (5)$$

The time-series component ($y_{L,t-j}$) included the prior year's characteristic in the focal lake ($y_{L,t-1}$) and any additional time lags that were significant in the T model (Eq. 3), while the spatial component includes information from neighboring lakes in the preceding year ($t-1$). Although this model is similar to the EC model (Eq. 3), it is distinctly different because current (t) characteristics of neighboring lakes are not included and all significant time lags identified in the T model are included instead of only the prior year's state of the focal lake. Thus, this model is a pure forecasting model that integrates both time-series and spatial comparative data, while the EC model is a mixture of both interpolation and forecasting. As with differences in the C and EC models, if the additional parameters in the ET model are nonsignificant, the ET model performance will be identical to the simpler T model. We interpret changes in model performance (defined below) and the composition of parameter types in ET models relative to the T models as a measure of the importance of the obtaining both types of forecasting data (spatial and temporal) and the relative importance of each type of data for making forecasts. As with the comparative models, MLR and AIC were used to determine the best combination of parameters (lake history and neighboring lakes) to predict the current annual value for each lake character-

istic. Similar to the comparative models, we also always selected the ET model with the lowest AIC value using a backward selection process.

Results

Example of model fitting—We fit 224 distinct models to data on eight variates in seven lakes for a time series of 22–28 yr (Web Appendix, Fig. A1, www.aslo.org/lo/toc/vol_57/issue_4/1113a.html). To illustrate the process, we present a detailed overview of the four models (C, EC, T, and ET) used to predict DOC characteristics in TB, which was chosen at random and does not represent the system where all models performed best. After this detailed presentation of a single variable in a single focal lake, we present an overview of the patterns of all eight variables in all seven lakes.

Comparative approach (Eq. 1): Average annual DOC concentrations in TB at year t were interpolated from a linear combination of the average annual DOC concentrations in the six neighboring lakes (AL, BM, CB, CR, SP, and TR) at year t . MLR was used to determine which neighboring lakes were the best predictors of TB DOC concentrations. Of all possible models, we selected the model with the lowest AIC value (−113.92) based on backward selection (Table 2). Five (AL, BM, CB, CR, and SP) of the six neighboring lakes were selected as significant predictors ($n = 22$, $r^2 = 0.89$, $F_{5,16} = 24.9$, $p < 0.001$). The standard deviation of prediction in-sample errors was 0.059, long-term annual mean DOC concentration was 2.96, and resulting prediction capacity was 0.020.

Enhanced Comparative approach (Eq. 3): Average annual DOC concentrations in TB at year t were predicted by a combination of interpolation using a linear combination of the average annual DOC concentrations in the six neighboring lakes (AL, BM, CB, CR, SP, and TR) at year t , and forecasting from the average annual DOC concentrations in the six neighboring lakes (AL, BM, CB, CR, SP, and TR) in the previous year (year $t-1$ along with TB (focal lake) average annual DOC concentration in the previous year (year $t - 1$). MLR was once again used to determine the set of best predictors for TB DOC concentrations. Of all possible models, we selected the model with the lowest AIC value (−121.17) based on backward selection (Table 2). Current characteristics (year t) of four (AL, BM, CR, and SP) of the six neighboring lakes, prior year characteristics (year $t - 1$) for two (BM and TR) of the six neighboring lakes, and the prior year characteristics (year $t - 1$) of TB (focal lake) were identified as significant predictors ($n = 21$, $r^2 = 0.95$, $F_{7,13} = 35.5$, $p < 0.001$). The standard deviation of prediction errors was 0.039, long-term annual mean DOC concentration was 2.97 (slightly different from the prior model because one less year is included in the time-series to account for 1-yr time lag), and resulting prediction capacity is 0.013.

Temporal (Eq. 4): Average annual DOC concentrations in TB at year t were forecasted from the history of DOC concentrations in TB using autocorrelation analyses. Concentration (year t) of DOC in TB was most significantly correlated with DOC concentrations at year $t - 1$ based on the ACF and PACF functions. After adding the

Table 2. Model coefficients for Comparative, Enhanced Comparative, Temporal, and Enhanced Temporal DOC predictive models in Trout Bog, Wisconsin, USA.

| Model | Predicting lake | Time lag | Model coefficient | <i>p</i> -value |
|----------------------|-----------------|-------------|-------------------|-----------------|
| Comparative | AL | <i>t</i> | 0.608 | 0.050 |
| | BM | <i>t</i> | -2.782 | <0.001 |
| | CB | <i>t</i> | 0.653 | 0.013 |
| | CR | <i>t</i> | 0.973 | <0.001 |
| | SP | <i>t</i> | 1.581 | 0.001 |
| Enhanced Comparative | AL | <i>t</i> | 0.770 | 0.003 |
| | BM | <i>t</i> | -1.164 | 0.027 |
| | CR | <i>t</i> | 0.460 | 0.041 |
| | SP | <i>t</i> | 0.591 | 0.059 |
| | BM | <i>t</i> -1 | 1.463 | 0.012 |
| | TR | <i>t</i> -1 | -1.432 | 0.060 |
| Temporal | TB | <i>t</i> -1 | 0.675 | <0.001 |
| | TB | <i>t</i> -2 | -0.504 | 0.031 |
| | TB | <i>t</i> -1 | 1.284 | <0.001 |
| Enhanced Temporal | SP | <i>t</i> -1 | 0.801 | 0.137 |
| | TR | <i>t</i> -1 | -1.039 | 0.170 |
| | TB | <i>t</i> -1 | 1.172 | <0.001 |
| | TB | <i>t</i> -2 | -0.525 | 0.026 |

1-yr time lag into the model and predicting annual DOC concentrations from the previous year's concentration, residual DOC concentrations were still significantly correlated at year $t - 2$. After adding the 2-yr time lag into the model, in addition to the previously included 1-yr time lag, residual DOC concentrations were no longer correlated at any time lags. Consequently, DOC concentrations in TB at year t were best forecasted by the combination of DOC concentrations in TB in the previous 2 yr (Table 2: $n = 20$, $r^2 = 0.81$, $F_{2,17} = 36.21$, $p < 0.001$). The standard deviation of prediction errors was 0.076, long-term annual mean DOC concentration was 2.98, and resulting prediction capacity is 0.026.

Enhanced Temporal approach (Eq. 5): This model forecasts current DOC concentrations in TB from past concentrations in TB and neighboring lakes. Average annual DOC concentrations in TB at year t were forecast from a 1-yr time lag in TB ($t - 1$), any additional time lags in TB quantified in the T model autocorrelation analysis (in this case a 2-yr lag), and average annual DOC concentrations in the six neighboring lakes (AL, BM, CB, CR, SP, and TR) in the previous year (year $t - 1$). MLR was used to determine which factors (lake history or neighboring lakes) were the best predictors of TB DOC concentrations. Of all possible models, we selected the model with the lowest AIC value (-98.13) based on backward selection (Table 2). The algorithm selected previous year's characteristics (year $t - 1$) of two (SP and TR) of the six neighboring lakes, and the two time lags in TB ($t - 1$ and $t - 2$) identified in the prior autocorrelation analysis ($n = 20$, $r^2 = 0.84$, $F_{4,15} = 20.1$, $p < 0.001$). The standard deviation of prediction errors was 0.069, long-term annual mean DOC concentration was 2.98, and resulting prediction capacity is 0.023.

In summary, for DOC in TB, the ranking of models (best to worst) based on prediction capacity is EC (0.013), C (0.020), ET (0.023), and T (0.026). Thus, the best model

(EC) is based on combination of interpolation and forecasting using data from neighboring lakes in years t and $t - 1$ plus the focal lake in the previous year. The worst model (T) considers only history of DOC in TB. The procedure outlined in the previous section was repeated for the remaining 220 models assessed in this study. The compositions of individual models are presented graphically in the Web Appendix, Figs. A2-A9.

Predictive model results—Variates had similar ranges in prediction capacity, but individual variables were predicted with differing levels of success (Fig. 2). Annual Ca concentrations were the most predictable (lowest median variation in prediction errors), while summer Chl concentrations were the least predictable (highest median variation in prediction errors; Fig. 2). Separated by limnological variable type, chemical variables were generally predicted with greater capacity than either the physical (Epi) or biological variables (Chl; Fig. 2).

Across all eight variables considered in this study, each variable was interpolated (C model) using, on average, observations from 2.6 of the neighboring six lakes (range = 0-5; Web Appendix, Figs. A2-A9). In ~ 7% of these models, data from neighboring lakes were unable to significantly interpolate the current state of a focal lake. Changes in prediction capacity as a function of training-dataset length were similar across all variables. Large increases in model performance were observed as training-dataset length increased from 8 yr to 12 yr (Fig. 3). Prediction capacity changed little relative to the prior changes for training datasets longer than 15 yr. Generally, the change in prediction capacity using combined in and out-of-sample errors between a 12-yr training dataset and the entire long-term record was similar in magnitude to the change observed between 10-yr and 12-yr training datasets (Fig. 3). This trend was also mirrored to the extent possible given the constraints this analysis imposed for the length of

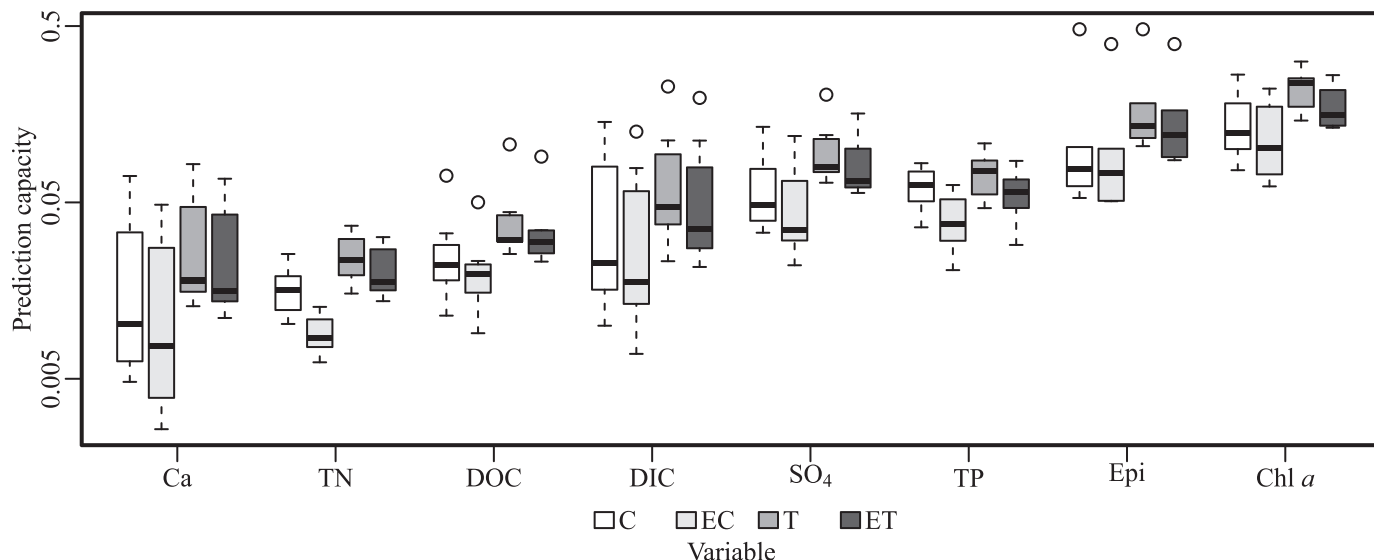


Fig. 2. Predictive capacity of Comparative (C), Enhanced Comparative (EC), Temporal (T), and Enhanced Temporal (ET) models for eight different variables. Ca = calcium, TN = total nitrogen, DOC = dissolved organic carbon, DIC = dissolved inorganic carbon, SO₄ = sulfate, TP = total phosphorus, Epi = epilimnetic depth, Chl *a* = chlorophyll *a*. Whiskers are 1.5× the inter-quartile range and outliers are denoted by open circles.

validation datasets when only out-of-sample errors were used to quantify the performance of the C models (Fig. 3). Results for Epi are similar, but not as consistent, and may be influenced by the fact that Epi is the least aggregated variate examined in this study.

Similar patterns were also observed in the sensitivity of the interpolation models to the specific observations used in the training datasets (i.e., the unique combination years selected from the entire record used to generate a potential training dataset). Interpolation models based on 8-yr training datasets were the most sensitive with large variances between potential training datasets, while variances decreased substantially with ≥ 10 -yr training datasets (Fig. 3). As with prediction capacity, the variation among potential training datasets stabilized in models based on ≥ 12 yr of training data (Fig. 3).

Including long-term historical observations into the model (i.e., EC model) increased the average number of lakes used to predict current dynamics in a focal lake by 1.6 lakes (Web Appendix, Figs. A2–A9). Additionally, past characteristics of the focal lake were significant predictors in 30% of the EC models, even when current dynamics of neighboring lakes were known. Overall, past characteristics of both the focal lake and neighboring lakes were significant predictors in 96% of EC models and resulted in a 29% (range –7% to 90%) increase in the prediction capacity differences between the EC and C models (Table 3). The decrease in model performance (–7%) in a single instance was the result of decreasing the number of years of data available in the model after accounting for time lags. Finally, integrating historical observations also reduced the number of interpolation models with no predictive capacity by $\sim 5\%$.

While the C and EC models were either pure interpolation models or a mix of forecasting and interpolation in the case of EC models, both the T and ET models are pure

forecasting models that differ based on whether or not the model integrates data from neighboring lakes. Very little autocorrelation was observed across the variables considered in this study, which resulted in poor performance of T models forecasting a lake's current state based on the long-term historical record in the focal lake. In 54% of T models, the past was not a significant predictor of the future (Web Appendix, Figs. A2–A9). When including forecasting parameters associated with both past characteristics of the focal lake and neighboring lakes (ET model), past characteristics of neighboring lakes were better forecasters of current lake characteristics in $\geq 52\%$ of the models. On average, data from 1.9 of the six neighboring lakes (range = 0–6) were used to generate forecasting predictions in ET models (Web Appendix, Figs. A2–A9). Additionally, in 38% of the prior T models with significant autocorrelation for focal-lake observations, the focal lake's parameter was not significant when neighboring lakes were included in the same ET model. This outcome was most notable for SO₄ (Web Appendix, Fig. A6) where the focal lake's history was dropped in four of the seven ET models. Overall, past characteristics of neighboring lakes were significant predictors in 90% of ET models and increased the difference in prediction capacity of ET models by as much as 54% (average 19%) relative to the corresponding T model (Table 3). Finally, including data from neighboring lakes reduced the number of pure forecasting models with no predictive capacity to $\sim 7\%$ (ET) compared with $\sim 54\%$ (T).

In most cases, the interpolation C model performed better than the forecasting T and ET models (Table 3; Figs. 2, 4). On average, C models were 45% and 28% better than either T or ET forecasting models, respectively, at predicting current focal-lake characteristics (Table 3). However, results also indicate that, in some cases, past characteristics of lakes can be equal or better predictors than are the current characteristics of neighboring lakes

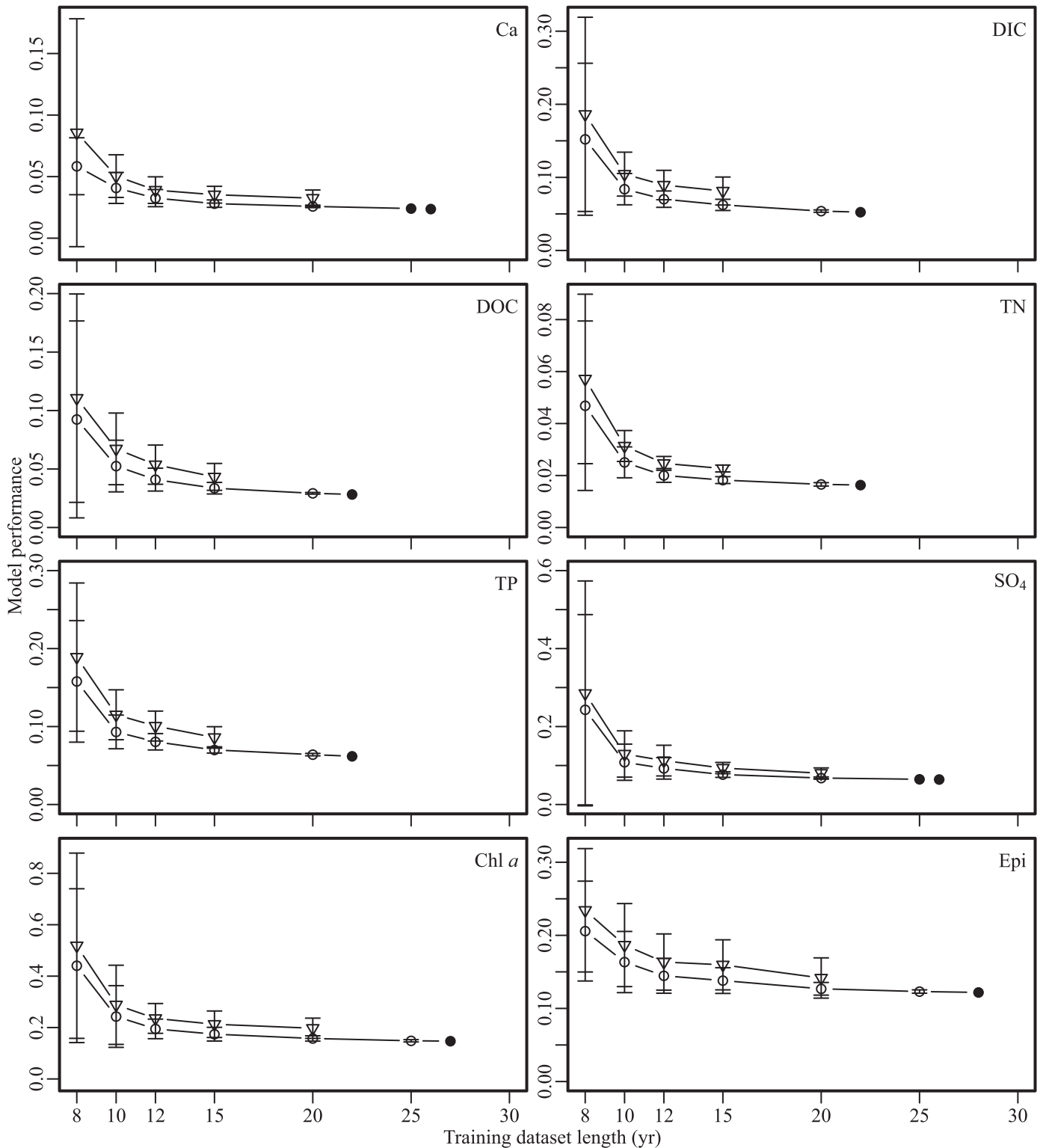


Fig. 3. Rarefaction analysis results for training datasets of different lengths. Error bars are one standard deviation and estimated using 100 unique potential training-dataset combinations. Prediction capacities calculated using both in and out-of-sample errors (i.e., entire record; open circles); prediction capacities calculated with < 100 unique year combinations (filled circles), and using only out-of-sample errors (i.e., only observations not used in the potential training dataset; triangles).

Table 3. Pairwise average relative percentage difference and range (worst, best) in predictive capacity for Comparative (C), Enhanced Comparative (EC), Temporal (T), and Enhanced Temporal (ET) models. Positive values indicate the relative percentage increase in model performance of the column model vs. the row model and vice versa for negative values.

| Models | C (%) | EC (%) | T (%) | ET (%) |
|--------|-------------|--------------|---------------|---------------|
| C | — | 29(−7, 90) | −45(−103, 5) | −28(−93, 24) |
| EC | −29(−90, 7) | — | −72(−133, −3) | −56(−128, 17) |
| T | 45(−5, 103) | 72(3, 133) | — | 19(0, 54) |
| ET | 28(−24, 93) | 56(−17, 128) | −19(−54, 0) | — |

(Fig. 4). This was most notable when examining the model performance of C and ET models, respectively (Fig. 4C). While, on average, the C model performed 28% better than the ET model, the ET model performed up to 24% better than the C model in several cases (Table 3; Fig. 4C). The most evident improvements were observed for TP, where six out of seven models were better predicted using pure forecasting approaches over pure interpolation approaches. We also observed a similar pattern in bog lakes, where ET models performed better than C models almost 50% of the time. Overall, approximately one-quarter of the forecasting ET models were better able to predict the current state of a focal lake than were interpolations using current dynamics in neighboring lakes (C model), and 31% of ET models were within 10% or better of their corresponding C models.

Discussion

Predictions of ecosystem variables are often a goal of sampling programs for both research and management (Pace 2001). Here, we focus on two different aspects of prediction, interpolation and forecasting in lake ecosystems. We provide an analysis of interpolation and forecasting for seven lakes over a 28-yr time frame. Analyses conducted demonstrate how much data is needed to interpolate lake characteristics in these systems, the importance of long-term data for generating interpolation and forecasting predictions, and key differences in the ability of interpolation and forecasting models to predict lake conditions.

Results from interpolation analyses were mixed with regard to how many different lakes are needed to interpolate the unknown state of a focal lake. Overall, very few neighboring lakes were needed in any specific model, but the composition of the models (i.e., which lakes were included) varied widely. No single lake or combination of lakes provided consistent predictions (Lottig 2009), and data from several neighboring systems appear to be necessary to develop predictive relationships. After predictive relationships are identified, monitoring of all lakes could be adjusted to serve a single predictive model, but this adjustment might come at the expense of predicting multiple variables and/or lakes. Our analyses also demonstrated the need for data to be collected over relatively long periods of time before interpolations stabilize. Rarefaction results consistently indicated that more than a decade of data is needed to maximize the effectiveness of interpolation models. Similar patterns have also been observed in maximum coherency between different lakes after about a decade as well (Magnuson et al. 2004). The stabilization in

variances among different training datasets indicates that data do not necessarily need to be continuous as long as the training datasets are of sufficient length.

The greatest gains in interpolation capacity were observed in the first several years of data collection. The lack of substantial improvements in prediction with training datasets longer than 12–15 yr suggests that interpolation potential is maximized (i.e., more data do not appear to refine the relationship between a focal lake and set of predictor lakes), and new data types are needed to realize further improvements in prediction capacity. Pure interpolation models, such as the C model presented here, are limited in that they have no historical context (Magnuson 1990) even though historical context or memory within lakes can be important for understanding long-term trends (Montgomery and Reckhow 1984). We found that prediction capacity increased measurably in the combination of interpolation and forecasting parameters (i.e., including historical context). A key step in predicting ecological characteristics is identifying interactions between space and time (Magnuson et al. 2006b), and it was through the combination of interpolation (space) and forecasting (time) that we were able to observe increases in relative prediction capacity. While significant increases in prediction capacity were observed through integrating both interpolation and forecasting approaches, those increases require a greater commitment to collecting continuous data due to the time series nature (i.e., historical context necessitates knowing the state at previous time steps) of forecasting parameters.

In cases where current information from other systems is not available to interpolate lake characteristics or where this type of data is inappropriate (e.g., lack of synchrony among systems) for generating predictions, predictions can be forecast using only historical observations. However, we found that, in almost all cases, forecasting models based solely on historical data from a focal lake (T models) performed worse than other models tested. The lack of consistent predictability with focal-lake history was related to the weak historical trends seen in this dataset. Lake characteristics in this study often vary substantially on a yearly basis and most of the time series exhibited low autocorrelation and few trends or big events that would help calibrate history-based forecasting models. Nonetheless, the ineffectiveness of most simple forecasting models is not necessarily evidence that these models should always be discarded. Instead, the effectiveness of simple forecasting models may depend largely on the type of variable and/or lake being considered. Limnological variables do not

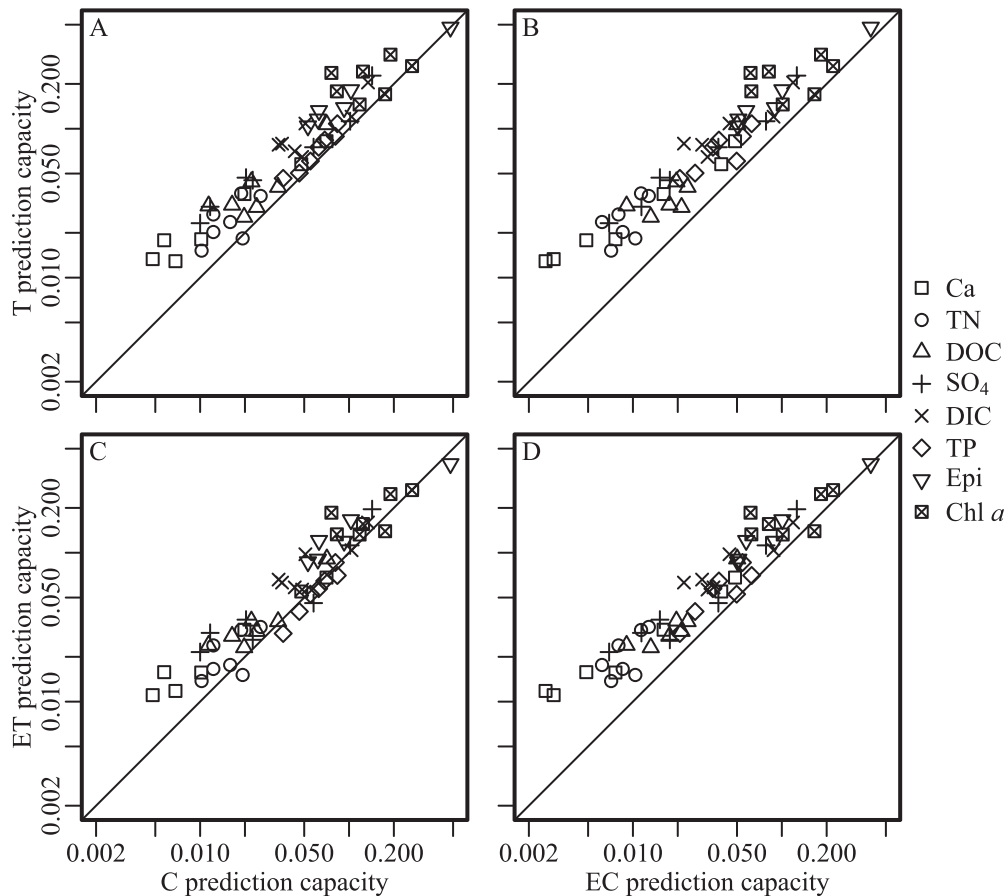


Fig. 4. Bivariate comparison plots of all Comparative (C), Enhanced Comparative (EC), Temporal (T), and Enhanced Temporal (ET) model-prediction capacities. Each point represents a lake-variable combination for the models considered (variable identity denoted by symbol). Points plotted left of the 1 : 1 line indicated that either the C or EC models performed better than forecasting models (T and ET) and vice versa for points right of the 1 : 1 line. Points situated along the 1 : 1 line have similar prediction capacities.

always vary in a similar fashion among lakes, even adjacent ones (Kratz et al. 1998), and forecasting models may be the best approach in some cases. For example, community interactions can lead to trends or cyclic changes that could be used to predict lake characteristics (Sanderson 1998; Sanderson et al. 1999; Beisner et al. 2003). In Crystal Lake (focal lake in this study), as much as 78% of the variation in chlorophyll concentrations can be explained by serial autocorrelation in the data (this study, Baines et al. 2000). We also observed more serial autocorrelation in bog lakes and seepage lakes than in drainage lakes (Lottig 2009). Thus, situations with weak external forcing, whether it is due to biology or low connectivity to the broader landscape, appear to be cases where historical information can facilitate predictions.

For systems and/or variates where historical data are not autocorrelated, adding forecasting information from neighboring systems may increase prediction capacity, as was observed in EC models. Lakes are often thought of as sentinels of change (Carpenter 1988; Williamson et al. 2008), and if different lakes respond to large-scale changes at unique time scales, individual lakes may help forecast

how other lakes will change in the future. In this study, substantial increases in forecasting ability were observed by including spatial forecasting parameters associated with neighboring lakes (ET models). Overall, we observed that approximately one in four enhanced forecasting models outperformed models based solely on interpolations from current conditions in surrounding systems, which is not a trivial improvement when attempting to generate the best prediction possible. However, it is important to also note that the data requirements for ET models are the most extensive of any model analyzed in this study, and thus this additional prediction capacity comes at a cost. As with T models where historical context in a focal lake can be important, historical context at the landscape level can be more important than current conditions in those same lakes for generating predictions of variables with known internal drivers (e.g., TP—6 out of 7 models; Soranno et al. 1997) and in lakes without strong long-term drivers (e.g., bog lakes—7 out of 16 models; Hanson et al. 2006).

The need to predict ecosystem characteristics is likely to rise as research initiatives increasingly focus on regional to global scales, and much is yet to be learned about how lake

characteristics can be upscaled (spatially and temporally) in different regions and at varying scales (Downing 2009). The lakes in this study are all located within a few km of one another and the strength of the interpolation models may, in part, be due to their close proximity. However, proximity of lakes and streams has been shown to matter little across relatively large spatial gradients for the synchrony of several variables analyzed here (e.g., Ca, DOC, SO₄; Folster et al. 2005; Evans et al. 2010), which suggests that similar results may be observed in other regions and at larger spatial scales than considered here. Lake variables also vary on time scales from minutes to decades (Hanson et al. 2006), and it is not clear whether the annual-scale patterns that we found would occur at other time scales. Interesting interplays between interpolation and forecasting models are likely to occur if strong periodicity or autocorrelation is observed in variables at unique time scales. The temporal resolution of prediction models may also have important implications with respect to the extent of data needed to generate predictions. Twelve to fifteen years of data (i.e., observations for annually resolved data) for interpolations and likely >30 yr, given the low autocorrelation in existing datasets, for simple forecasting models were needed in this study. However, if sufficient shared variation among, or autocorrelation within, lakes is observed at higher temporal frequencies (e.g., monthly or quarterly), future studies may not necessarily need a decade or more to develop lake prediction models similar to the ones examined in this study.

Further increases in prediction capacity could arise from introducing new types of predictor variables or from large perturbations that expose new kinds of lake dynamics. More complex modeling approaches could potentially increase prediction capacity by incorporating other drivers, such as landscape characteristics, hydrology, climate, and/or relevant biogeochemical processes. However, increasing model complexity does not always result in measurable increases in prediction capacity, and simple models are necessary for broad extrapolation of patterns to unmeasured systems (Debra et al. 2004). Effective models for predicting lake characteristics likely need to include simple sets of predictor variables that are easily attainable. The work presented here provides one example, using lakes, of how comparative and temporal data could be applied in studies where similar systems are monitored for several years to generate predictions of ecosystems characteristics in space and time.

We provided an analysis of interpolation and forecasting predictions in seven lakes over a 28-yr time frame. We found that interpolation generally provided better predictions than did forecasting when relying on one approach. However, we also found that a decade or more of training data was needed to generate the most effective interpolation models. At annually resolved timescales, our results also demonstrated that collecting long-term, continuous data could enhance interpolation predictions. Substantial increases in prediction capacity were observed when forecasting parameters (i.e., historical context) were included in interpolation models, which is only possible with continuous long-term data. Moreover, collecting this type

of data allowed us to identify variables and systems where pure forecasting models were more effective than basic interpolation models through model comparisons and the flexibility to switch between approaches when necessary in order to generate the best predictions possible with available data. Overall, both interpolation and forecasting techniques were needed to generate the best predictions. Relying on a single approach would have limited prediction capacity for the variables and systems considered in this study.

Although generating the best predictions possible is desirable, this study identified key trade-offs with respect to the types of data collected for generating these predictions. Basic interpolation models, such as those presented here, are simpler than either pure forecasting or mixed interpolation and forecasting models because time is not incorporated in these models. Constructing basic interpolation models does not require continuous data for calibration and may not require data to be collected in perpetuity. Thus, interpolation approaches might allow sampling and prediction efforts to be spread out over a greater number of systems. On the other hand, our data also demonstrate that better predictions can be generated by collecting long-term, continuous data because lakes do not always vary in a similar fashion, historical context is important, and, for some variables and systems, forecasting approaches are more effective than interpolation. However, generating the best predictions required the greatest commitment to collecting long-term, continuous data, and availability of resources could limit the number of systems in which these types of models could be applied.

Long-term and spatially extensive views are needed to understand complex systems (Magnuson et al. 2006b). Many important changes in ecosystems are important precisely because they are not predictable from the past and often only become apparent with a long-term perspective (Webster et al. 1996, 2000). Prediction of change is a fundamentally different problem from detection of change (Magnuson 1990; Magnuson et al. 2000; Carpenter et al. 2007). Because ecosystems are changing more rapidly now than ever before (MA 2005), the detection of new trends and prediction of how systems may change in the future will depend on ongoing collection of long-term and spatially extensive data. Basic monitoring data has the potential to be upscaled to generate predictions of lake characteristics, but the effectiveness of predictions depend on the training-data characteristics and prediction approaches employed.

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References

- AHLGREN, I., T. FRISK, AND L. KAMP-NEILSEN. 1988. Empirical and theoretical models of phosphorus loading, retention, and concentration vs. lake trophic state. *Hydrobiologia* **170**: 285–303, doi:10.1007/BF00024910
- ANDERSON, N. J. 1995. Using the past to predict the future: Lake sediments and the modeling of limnological disturbance. *Ecol. Model.* **78**: 149–172, doi:10.1016/0304-3800(94)00124-Z
- BAINES, S. B., K. E. WEBSTER, T. K. KRATZ, S. R. CARPENTER, AND J. J. MAGNUSON. 2000. Synchronous behavior of temperature, calcium, and chlorophyll in lakes of northern Wisconsin. *Ecology* **81**: 815–825, doi:10.1890/0012-9658(2000)081[0815:SBOTCA]2.0.CO;2
- BEISNER, B. E., A. R. IVES, AND S. R. CARPENTER. 2003. Effects of an exotic fish invasion on the prey communities of two lakes. *J. Anim. Ecol.* **72**: 331–342, doi:10.1046/j.1365-2656.2003.00699.x
- CARDILLE, J. A., S. R. CARPENTER, M. T. COE, J. A. FOLEY, P. C. HANSON, M. G. TURNER, AND J. A. VANO. 2007. Carbon and water cycling in lake-rich landscapes: Landscape connections, lake hydrology, and biogeochemistry. *J. Geophys. Res.* **112**: G02031, doi:10.1029/2006/JG000200
- CARPENTER, S. R. [ED.]. 1988. Complex interactions in lake communities. Springer-Verlag.
- , AND OTHERS. 2007. Understanding regional change: Comparison of two lake districts. *BioScience* **57**: 323–335, doi:10.1641/B570407
- CHATFIELD, C. 1980. The analysis of time series: An introduction, 2nd ed. Chapman and Hall.
- COLE, J. J., G. LOVETT, AND S. G. FINDLAY [EDS.]. 1991. Comparative analyses of ecosystems. Springer-Verlag.
- DEBRA, P. C., J. E. HERICK, D. L. URBAN, R. H. GARDNER, AND D. D. BRESHEARS. 2004. Strategies for ecological extrapolation. *Oikos* **106**: 627–636, doi:10.1111/j.0030-1299.2004.12869.x
- DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relation in lakes. *Limnol. Oceanogr.* **19**: 767–773, doi:10.4319/lo.1974.19.5.0767
- DOWNING, J. A. 2009. Global limnology: Up-scaling aquatic services and processes to planet earth. *Verh. Interna. Verein. Limnol.* **30**: 1149–1166.
- , S. B. WATSON, AND E. McCAULEY. 2001. Predicting cyanobacteria dominance in lakes. *Can. J. Fish. Aquat. Sci.* **58**: 1905–1908, doi:10.1139/f01-143
- EVANS, C. D., AND OTHERS. 2010. Linking monitoring and modeling: Can long-term datasets be used more effectively as a basis for large-scale prediction. *Biogeochemistry* **101**: 211–227, doi:10.1007/s10533-010-94130-x
- FEE, E. J., AND R. E. HECKY. 1992. Introduction to the northwest Ontario lake size series (NOLSS). *Can. J. Fish. Aquat. Sci.* **49**: 2434–2444, doi:10.1139/f92-269
- FOLSTER, J., E. GORANSSON, K. JOHANSSON, AND A. WILANDER. 2005. Synchronous variation in water chemistry for 80 lakes in southern Sweden. *Environ. Monit. Assess.* **102**: 389–403, doi:10.1007/s10661-005-6394-7
- FRATERRIGO, J. M., AND J. A. DOWNING. 2008. The influences of land use on lake nutrients varies with watershed transport capacity. *Ecosystems* **11**: 1021–1034, doi:10.1007/s10021-008-9176-6
- GEORGE, D. G., J. F. TALLING, AND E. RIGGS. 2000. Factors influencing the temporal coherence of five lakes in the English Lake District. *Freshw. Biol.* **43**: 449–461, doi:10.1046/j.1365-2427.2000.00566.x
- HANSON, P. C., S. R. CARPENTER, D. E. ARMSTRONG, E. H. STANLEY, AND T. K. KRATZ. 2006. Lake dissolved inorganic carbon and dissolved oxygen: Changing drivers from days to decades. *Ecol. Monogr.* **76**: 343–363, doi:10.1890/0012-9615(2006)076[0343:LDICAD]2.0.CO;2
- , ———, J. A. CARDILLE, M. T. COE, AND L. A. WINSLOW. 2007. Small lakes dominate a random sample of regional lake characteristics. *Freshw. Biol.* **52**: 814–822, doi:10.1111/j.1365-2427.2007.01730.x
- IVES, A. R. 1995. Predicting the response of populations to environmental change. *Ecology* **76**: 926–941, doi:10.2307/1939357
- KRATZ, T. K., P. A. SORANNO, S. B. BAINES, B. J. BENSON, J. J. MAGNUSON, T. M. FROST, AND R. C. LATHROP. 1998. Interannual synchronous dynamics in north temperate lakes in Wisconsin, p. 273–287. *In* D. G. George, J. G. Jones, P. Puncochar, C. S. Reynolds, and D. W. Sutcliffe [eds.], *Management of lakes and reservoirs during global climate change*. Kluwer Academic.
- LIKENS, G. E., [ED.]. 1989. Long-term studies in ecology: Approaches and alternatives. Springer-Verlag.
- LOTTIG, N. R. 2009. Regional aquatic biogeochemistry of the Northern Highlands Lake District. Ph.D. thesis. Univ. of Wisconsin.
- , E. H. STANLEY, P. C. HANSON, AND T. K. KRATZ. 2011. Comparison of regional stream and lake chemistry: Differences, similarities, and potential drivers. *Limnol. Oceanogr.* **56**: 1551–1562, doi:10.4319/lo.2011.56.5.1551
- MAGNUSON, J. J. 1990. Long-term ecological research and the invisible present. *Bioscience* **40**: 495–501, doi:10.2307/1311317
- , B. J. BENSON, AND T. K. KRATZ. 2004. Patterns of coherent dynamics within and between lake districts at local to intercontinental scales. *Boreal Environ. Res.* **9**: 359–369.
- , T. K. KRATZ, AND B. J. BENSON [EDS.]. 2006a. Long-term dynamics of lakes in the Landscape. Oxford Univ. Press.
- , ———, AND ———. 2006b. The challenge of time and space in ecology, p. 3–16. *In* J. J. Magnuson, T. K. Kratz, and B. J. Benson [eds.], *Long-term dynamics of lakes in the landscape: Long-term ecological research on north temperate lakes*. Oxford Univ. Press.
- , ———, ———, AND K. E. WEBSTER 2006c. Coherent dynamics among lakes, p. 89–106. *In* J. J. Magnuson, T. K. Kratz, and B. J. Benson [eds.], *Long-term dynamics of lakes in the landscape: Long-term ecological research on north temperate lakes*. Oxford Univ. Press.
- MAGNUSON, J. J., AND OTHERS. 2000. Historical trends in lake and river ice cover in the northern hemisphere. *Science* **289**: 1743–1746, doi:10.1126/science.289.5485.1743
- MILLENNIUM ECOSYSTEM ASSESSMENT [MA]. 2005. Ecosystem human well-being: Current states and trends. Island Press.
- MONTGOMERY, R. H., AND K. H. RECKHOW. 1984. Techniques for detecting trends in lake water quality. *J. Am. Water Res. As.* **20**: 43–52, doi:10.1111/j.1752-1688.1984.tb04640.x
- PACE, M. L. 2001. Prediction and the aquatic sciences. *Can. J. Fish. Aquat. Sci.* **58**: 63–72, doi:10.1139/f00-151
- PETERS, R. H. 1986. The role of prediction in limnology. *Limnol. Oceanogr.* **31**: 1143–1160, doi:10.4319/lo.1986.31.5.1143
- ROBERTSON, D. M., AND R. A. RAGOTZKIE. 1990. Change in the thermal structure of moderate to large sized lakes in response to change in air temperature. *Aquat. Sci.* **52**: 360–380, doi:10.1007/BF00879763
- SANDERSON, B. L. 1998. Factors regulating water clarity in northern Wisconsin lakes. Ph.D. thesis. Univ. of Wisconsin.
- , T. R. HRABIK, J. J. MAGNUSON, AND D. M. POST. 1999. Cyclic dynamics of a yellow perch (*Perca flavescens*) population in an oligotrophic lake: Evidence for the role of intraspecific interactions. *Can. J. Fish. Aquat. Sci.* **56**: 1534–1542.
- SORANNO, P. A., S. R. CARPENTER, AND R. C. LATHROP. 1997. Internal phosphorus loading in Lake Mendota: Response to external loads and weather. *Can. J. Fish. Aquat. Sci.* **54**: 1883–1893.

- , S. L. HUBLER, S. R. CARPENTER, AND R. C. LATHROP. 1996. Phosphorus loads to surface waters: A simple model to account for spatial pattern of land use. *Ecology* **6**: 865–878.
- VOGT, R. J., J. A. RUSAK, A. PATOINE, AND P. R. LEAVITT. 2011. Differential effects of energy and mass influx on the landscape synchrony of lake ecosystems. *Ecology* **92**: 1104–1114, doi:10.1890/i0012-9658-92-5-1104
- VOLLENWEIDER, R. A. 1969. Possibilities and limits of elementary models concerning the budget of substances in lakes. *Arch. Hydrobiol.* **66**: 1–36.
- WEBSTER, K. E., C. J. BOWSER, M. P. ANDERSON, AND J. D. LENTERS. 2006. Understanding the lake–groundwater system: Just follow the water, p. 19–48. *In* J. J. Magnuson, T. K. Kratz, and B. J. Benson [eds.], *Long-term dynamics of lakes in the landscape: Long-term ecological research on north temperate lakes*. Oxford Univ. Press.
- , T. K. KRATZ, C. J. BOWSER, J. J. MAGNUSON, AND W. J. ROSE. 1996. The influence of landscape position on lake chemical responses to drought in northern Wisconsin. *Limnol. Oceanogr.* **41**: 977–984, doi:10.4319/lo.1996.41.5.0977
- , AND OTHERS. 2000. Structuring features of lake districts: Landscape controls on lake chemical responses to drought. *Freshw. Biol.* **43**: 499–515, doi:10.1046/j.1365-2427.2000.00571.x
- WILLIAMSON, C. E., W. DODDS, T. K. KRATZ, AND M. A. PALMER. 2008. Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. *Front. Ecol. Environ.* **6**: 247–254, doi:10.1890/070140

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