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Title: Using near-term forecasts and uncertainty partitioning to improve predictions of low-frequency cyanobacterial events

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Abstract

Near-term ecological forecasts provide resource managers advance notice of changes in ecosystem services, such as fisheries stocks, timber yields, or water and air quality. Importantly, ecological forecasts can identify where uncertainty enters the forecasting system, which is necessary to refine and improve forecast skill and guide interpretation of forecast results. Uncertainty partitioning identifies the relative contributions to total forecast variance (uncertainty) introduced by different sources, including specification of the model structure, errors in driver data, and estimation of initial state conditions. Uncertainty partitioning could be particularly useful in improving forecasts of high-density cyanobacterial events, which are difficult to predict and present a persistent challenge for lake managers. Cyanobacteria can produce toxic or unsightly surface scums and advance warning of these events could help managers mitigate water quality issues. Here, we calibrate fourteen Bayesian state-space models to evaluate different hypotheses about cyanobacterial growth using data from eight summers of weekly cyanobacteria density samples in an oligotrophic (low nutrient) lake that experiences sporadic surface scums of the toxin-producing cyanobacterium, *Gloeotrichia echinulata*. We identify dominant sources of uncertainty for near-term (one-week to four-week) forecasts of *G. echinulata* densities over two years. Water temperature was an important predictor in calibration and at the four-week forecast horizon. However, no environmental covariates improved over a simple autoregressive (AR) model at the one-week horizon. Even the best fit models exhibited large variance in forecasted cyanobacterial densities and often did not capture rare peak density occurrences, indicating that significant explanatory variables in calibration are not always effective for near-term forecasting of low-frequency events. Uncertainty partitioning revealed that model process specification and initial conditions uncertainty dominated forecasts at both

time horizons. These findings suggest that observed densities result from both growth and movement of *G. echinulata*, and that imperfect observations as well as spatial misalignment of environmental data and cyanobacteria observations affect forecast skill. Future research efforts should prioritize long-term studies to refine process understanding and increased sampling frequency and replication to better define initial conditions. Our results emphasize the importance of ecological forecasting principles and uncertainty partitioning to refine and understand predictive capacity across ecosystems.

Keywords: Bayesian model, blooms, dynamic linear model, ecological forecasting, hindcast, lake, oligotrophic, phytoplankton, scums, state-space model, uncertainty partitioning, variance partitioning

I. Introduction

Near-term ecological forecasts, defined as daily to decadal predictions of the state of ecosystems (Clark et al. 2001, Dietze et al. 2018), can be helpful to resource managers in systems ranging from fisheries stocks to disease outbreaks in protected species populations (Kuikka et al. 2014, Hobbs et al. 2015). For example, near-term forecasts have been used to provide projections for alternate management decisions (Kuikka et al. 2014, Thomas et al. 2018, 2020), help managers allot fisheries take quotas (or used to avoid bycatch; Hobday et al. 2019 and references therein), and provide advance notice of public safety hazards such as red tides (Stumpf et al. 2009, McGowan et al. 2017). Effective near-term forecasts include fully-specified uncertainty by quantifying the total variance around a prediction and identifying the relative

contributions of different sources of uncertainty (Dietze et al. 2018; Box 1).

Uncertainty in ecological forecasts may arise from several different sources, including: initial conditions uncertainty, parameter uncertainty, process uncertainty, observation uncertainty, driver or covariate data uncertainty, and random effects uncertainty (Dietze 2017a; Table 1). Partitioning the variance associated with a forecast into these components allows for more targeted efforts to understand and improve forecasts. For example, the dominant contributor to uncertainty in weather forecasts is from initial conditions because the atmosphere's internal instability amplifies even small errors in initial condition estimates and the physical processes controlling weather given a set of current conditions are relatively well-defined (Dietze 2017b). This has directed weather forecasters to prioritize efforts to better measure starting atmospheric conditions (Shuman 1989, Bauer et al. 2015). In contrast, the dominance of process uncertainty in a forecast indicates that researchers need to consider alternative model structures and additional or different explanatory variables to describe the biological or ecological process of interest (Page et al. 2017, Thomas et al. 2018). Formal, standardized uncertainty partitioning can guide improvements to ecological forecasts and ultimately lead to more informed management of natural resources (Bauer et al. 2015, Page et al. 2018).

Estimating uncertainty has become more common in ecological analyses that generate forecasts (see studies in Table S1 for examples). However, formal uncertainty partitioning that includes all the potential sources of forecast uncertainty is less common and methods are not standardized, making it difficult to compare how different components of uncertainty contribute across ecological systems or among focal state variables. For example, while studies by Gertner et al. 1996, Valle et al. 2009, Wang et al. 2009, and Thomas et al. 2018 (Table S1) all forecast

different metrics of forest biomass and productivity, differences in how they estimate and partition uncertainty limit synthetic understanding of the predominance of process structure or estimation of drivers or parameters to uncertainty in forecasts about forest productivity.

Forecasting freshwater cyanobacterial dynamics has been a persistent challenge for researchers and water quality managers (Janssen et al. 2019, Rousso et al. 2020), and uncertainty partitioning analysis could help refine and advance forecasting capacity in this system. Cyanobacteria are increasing in many lakes and reservoirs worldwide due to climate and land-use change, posing substantial problems for drinking water managers and other stakeholders (Schindler and Vallentyne 2008, Paerl et al. 2011, Carey et al. 2012b, O'Neil et al. 2012). Many cyanobacterial taxa create toxic or unsightly scums that cause taste and odor problems and clog filters at drinking water treatment plants; consequently, knowing when cyanobacterial density is likely to increase could allow managers to take pre-emptive action to mitigate deleterious water quality effects (van Dolah et al. 2015, Ibelings et al. 2016, Stroom and Kardinaal 2016). However, despite substantial research on drivers of cyanobacterial dominance (e.g., Carey et al. 2012b, Paerl and Otten 2013) and recent technological developments permitting high-frequency observations of cyanobacterial density (e.g., Le Vu et al. 2011, Catherine et al. 2012), near-term cyanobacterial abundance model predictions often deviate substantially from observations (Hamilton et al. 2009, Rigosi et al. 2010, Reynolds et al. 2014, Janssen et al. 2019) and few studies have examined forecast uncertainty (Rousso et al. 2020; but see Huang et al. 2013, Page et al. 2017, Massoud et al. 2018). The challenges in forecasting cyanobacteria may be attributable to the rate of cyanobacterial growth relative to the frequency of most sampling campaigns. Cyanobacterial densities can change rapidly on timescales of days to weeks (Dokulil and Teubner 2000, Huisman and Hulot 2005, Rolland et al. 2013, Carpenter et al. 2020), with

densities in many lakes remaining relatively low for much of the year and then rapidly increasing from one sample period to the next (e.g., Bormans et al. 2005, Rolland et al. 2013, Carey et al. 2014a).

Cyanobacterial blooms are often associated with high nutrient levels (Dokulil and Teubner 2000), and so much of the effort to predict cyanobacterial densities has been focused on nutrient-rich lakes (Rousso et al. 2020). As a result, prediction efforts for high-density cyanobacterial events in oligotrophic lakes have lagged behind, and understanding why cyanobacterial densities change over the short term in low-nutrient lakes is especially challenging. However, teasing apart the different sources of uncertainty and their relative importance to cyanobacterial forecast precision may help prioritize research efforts in economically important oligotrophic waterbodies. Increases in the occurrence of high-density cyanobacterial events have been documented in north temperate oligotrophic lakes throughout the United States (Carey et al. 2012a), Canada (Winter et al. 2011), and Europe (Freeman et al. 2020), and these increases are often associated with significant economic losses and public health concerns (Dodds et al. 2009, Mueller et al. 2016, Stoddard et al. 2016). High water quality in oligotrophic lakes provides substantial economic benefit through recreational use and high lakeside property values (Wilson and Carpenter 1999, Dodds et al. 2009, Mueller et al. 2016, Stoddard et al. 2016). Moreover, some oligotrophic systems are permitted as drinking water sources with reduced filtration requirements when their water quality meets United States Environmental Protection Agency (U.S. EPA) standards, thereby reducing water treatment costs (U.S. EPA 1991, Kauffman 2016, Ravindranath et al. 2016).

Prior studies provide several hypotheses for what environmental drivers likely trigger cyanobacterial growth or accumulation of cyanobacterial surface scums, including: increased

159 growth at higher temperatures (Paerl and Huisman 2008, Hamilton et al. 2009); light-induced
160 triggering of cell germination and growth (Roelofs and Oglesby 1970, Karlsson-Elfgren et al.
161 2004); more recruitment of dormant cells from the sediment and/or dilution of surface water
162 cyanobacterial density due to water column mixing, which can occur due to temperature
163 changes, precipitation events, or wind (Jennings et al. 2012, Carey et al. 2014, de Eyto et al.
164 2016, Kuha et al. 2016); greater incidence of surface scums during periods of stronger thermal
165 stratification (Carey et al. 2012b); and aggregation of cells or colonies in nearshore zones by
166 wind (Roelofs and Oglesby 1970, Cyr 2017). The development of forecast models with
167 uncertainty partitioning is needed to compare and evaluate these hypotheses in a predictive
168 framework.

169 While there are a variety of techniques that can be used to develop forecast models with
170 partitioned uncertainty, Bayesian state-space models are particularly suitable (Clark 2007, Hobbs
171 and Hooten 2015, Dietze 2017a). State-space models focus on estimating the true, latent state of
172 the system by explicitly accounting for observation and process uncertainty. These dynamic
173 models are structured so that each modeled latent state is a function of the previous latent state,
174 independent of observations at other time points (Hobbs and Hooten 2015, Dietze 2017a; Fig. 1).
175 Bayesian state-space models use distributions rather than fixed values to represent all unknown
176 values, including parameters, initial conditions, and as-yet-unobserved future values for driver
177 variables, allowing for quantification of uncertainty associated with each of these components
178 and missing data.

179 We developed and evaluated a suite of Bayesian state-space models with different
180 structures and tested different environmental variables hypothesized to be important in driving
181 cyanobacterial density, including water temperature, thermal stability, wind, and light. We

calibrated each model to weekly cyanobacterial densities measured from 2009-2014 in Lake Sunapee, NH, USA, an oligotrophic lake that exhibits variable densities of the toxin-producing cyanobacterium *Gloeotrichia echinulata*. We then generated hindcasts (defined in Table 1) of cyanobacterial density for 2015-2016. We assessed and conducted uncertainty partitioning of our hindcasts to address the following questions: A) Which model structures and environmental covariates best predict oligotrophic lake cyanobacterial density over one to four week forecast horizons? B) What are the dominant sources of uncertainty in oligotrophic lake cyanobacterial forecasts? and C) How do the relative contributions of different sources of uncertainty vary among models with differing complexity and environmental covariates? We discuss how our results inform future efforts to forecast oligotrophic lake cyanobacterial density and relate to patterns of predictive uncertainty observed in other ecosystems.

II. Methods

Focal cyanobacterium

Gloeotrichia echinulata is a colonial, filamentous cyanobacterium commonly found in oligotrophic north temperate lakes in the United States, Canada, and Europe (Karlsson-Elfgren et al. 2005, Winter et al. 2011, Carey et al. 2012a, Freeman et al. 2020). *G. echinulata* is capable of forming surface scums and producing toxins (Karlsson-Elfgren et al. 2005, Carey et al. 2012a). Occurrence of *G. echinulata* surface scums in oligotrophic north temperate lakes has been increasing in recent decades (Carey et al. 2008, 2012a, Winter et al. 2011), motivating researchers to improve understanding and prediction of *G. echinulata* density in these ecosystems. While nutrients are often a driver of cyanobacterial growth in eutrophic lakes

(Dokulil and Teubner 2000), current understanding of dynamics in oligotrophic systems suggests that other environmental drivers may be important for determining *G. echinulata* densities (Roelofs and Oglesby 1970, Karlsson-Elfgren et al. 2004, Carey et al. 2014, Cyr 2017).

Study site

We sampled *G. echinulata* surface abundance and collected environmental data weekly in May-October from 2009-2016 at two nearshore sites in Lake Sunapee, NH, USA, a recreational lake with high property values that also serves as a public drinking water supply (Fig. 2). Lake Sunapee is a large, oligotrophic lake (lat 43°24′N, long 72°2′W, max. depth = 33.7 m, surface area = 16.69 km^2, volume = 1.94 × 10 m^3, mean depth = 11.6 m, Lake Sunapee Protective Association (LSPA), unpublished data). High-nutrient (eutrophic) lakes can have total phosphorus (TP) concentrations ≥ 24 μg L^{-1} and total nitrogen (TN) concentrations ranging from ~400-1600 μg L^{-1} (Carlson 1977, Carlson and Simpson 1996, Gibson et al. 2000). Mean TP concentration in the surface waters of Lake Sunapee between 2009-2016 was 6.3 ± 1.7 μg L^{-1} (mean ± 1 S.D.), and mean Secchi depth was 6.6 ± 0.6 m (LSPA, unpub. data). Mean TN concentration from 2009-2012 at our study site was 172 ± 25 μg L^{-1} (Cottingham 2020). Lake Sunapee typically thermally stratifies from June-September with a mean thermocline depth of 7-9 m from 2009-2016. The watershed (~107 km^2 not including lake surface area) is 80% forested but shoreline development has been increasing in recent decades (Cobourn et al. 2018).

Our research team began a weekly *G. echinulata* monitoring program at two sampling sites in collaboration with the Lake Sunapee Protective Association (LSPA) in 2005 (Carey et al. 2008, 2014b). Our focal sampling site for this study (Site 1; Fig. 2) was chosen because it frequently exhibits high densities of *G. echinulata*. We used data from the second nearshore site

(Site 2) only to generate informed priors for *G. echinulata* observation error and nearshore water temperature and these data were not included in any hindcasting analyses. We focused our analyses on 2009-2016 for this study because those years had at least 20 weeks of sampling data (Cottingham et al. 2020a); however, during our eight-year study period there were six missing weekly *G. echinulata* observations, four of which occurred during the 2015-2016 hindcasting period.

G. echinulata data collection and sample processing

G. echinulata surface abundance at both nearshore sites was sampled each week in the top 1 m of the water column by combining two vertical tows from 1 m to the surface using a 30 cm diameter, 80 μm mesh plankton net (Wildlife Supply Co., Yulee, Florida). *G. echinulata* were transferred from the net and preserved in opaque plastic bottles using Lugol's iodine (Carey et al. 2014). Total *G. echinulata* samples were counted using a Leica MZ12 dissecting microscope (Leica, Buffalo Grove, Illinois). Density was quantified according to the number of colonies and filament bundles (immature, developing colonies) per liter rather than biovolume following protocols used in previous studies of *G. echinulata* (Roelofs and Oglesby 1970, Barbiero and Welch 1992, Karlsson-Elfgren et al. 2005). We then converted abundance to density by dividing the total number of colonies and filament bundles in each sample by the volume of water sampled by the plankton net (Carey et al. 2014b). All data are publicly available through the Environmental Data Initiative repository (Cottingham et al. 2020a, 2020b, LSPA et al. 2020a, 2020b; Lofton et al. 2020).

Environmental driver data

To capture the effect of temperature on *G. echinulata* growth, water temperature was monitored hourly using Onset loggers at our nearshore sampling sites (Sites 1 and 2; Fig. 2; Cottingham et al. 2020b). Growing degree days (GDD), a measure of heat accumulation during the growing season, were calculated using these water temperatures for each day when *G. echinulata* was sampled. To investigate effects of thermal stratification on *G. echinulata* surface density, water temperature profiles from the Global Lake Ecological Observatory Network (GLEON) buoy, deployed in the lake by the LSPA since 2007 (Site 3), were used to calculate Schmidt stability, a measure of thermal stratification strength that indicates the amount of energy required to homogenize temperature across the water column (Idso 1973, LSPA et al. 2020b). To examine whether wind could drive nearshore aggregation of *G. echinulata* colonies, wind data from the LSPA/GLEON buoy (Site 3) were aggregated from minute and hourly scales, respectively, to calculate daily summary statistics (LSPA et al. 2020a). Solar radiation data from the North American Land Data Assimilation System Phase 2 (NLDAS-2) forcing dataset (https://ldas.gsfc.nasa.gov/nldas; Lofton et al. 2020) and photosynthetically active radiation (PAR) data from the LSPA/GLEON buoy (LSPA et al. 2020a) were similarly aggregated to determine whether light was an important predictor of *G. echinulata* density. Finally, we calculated summary statistics of daily precipitation data from the Parameter-elevation Relationships on Independent Slopes Model (PRISM) model (http://www.prism.oregonstate.edu; Lofton et al. 2020) to examine the effect of storm events and subsequent water column mixing on *G. echinulata* pelagic populations (see Text S1 for further information on environmental data processing).

Selection of environmental covariates for Bayesian models

We performed a standardized selection process to determine which potential environmental drivers of *G. echinulata* density to include in Bayesian state-space models (Text S2). We examined associations between natural log-transformed *G. echinulata* density from 2009-2014 (calibration period) and 82 summary statistics of candidate environmental covariates identified as potential drivers in previous studies (Roelofs and Oglesby 1970, Karlsson-Elfgren et al. 2004, Paerl and Huisman 2008, Hamilton et al. 2009, Carey et al. 2012b, 2014, Jennings et al. 2012, de Eyto et al. 2016, Kuha et al. 2016, Cyr 2017). We used Spearman correlations to prioritize inclusion in our Bayesian models (Text S2). The full list of covariate summary statistics is in Table S2. This approach identified eight drivers for further evaluation (Table 2): daily minimum water temperature on the sampling day (MinWaterTemp), daily minimum water temperature with a one-week lag (MinWaterTempLag), seven-day moving average of water temperature (WaterTempMA), weekly difference in median Schmidt stability (ΔSchmidt), daily maximum Schmidt stability with a one-week lag (SchmidtLag), daily mean of a wind direction indicator variable with a two-day lag (WindDir; see Text S1 for details on wind indicator variable calculation), growing degree days (GDD), and daily sum of precipitation (Precip).

Development of Bayesian state-space models

A suite of Bayesian state space models were fit to data collected from Site 1 and increased in complexity from a random walk with no covariates (intercept model) to models containing one or two of the eight prioritized driver variables (Fig. 3; Table 2). We calibrated each model over a 6-year period from 2009-2014, assessed model performance during a two-year hindcasting period of 2015-2016, and then conducted uncertainty partitioning. We investigated

297 whether sequential increases in model complexity translated to changes in the relative
298 contributions of different uncertainty sources to total hindcast uncertainty, increases in skill of *G.*
299 *echinulata* density hindcasts, or both (Fig. 3; Table 2).
300 We assessed hindcast skill of the twelve models including environmental covariates
301 compared to two baseline models: first, a model with a random walk process and an informed
302 prior for observation error developed using data from Site 2 (RW model; Fig. 3; Text S3), and
303 second, a linear autoregressive process model with a single lag (AR model; Fig. 3; Table 2). We
304 also assessed a random walk model with a random year effect as a possible baseline model but
305 determined during model calibration that the estimated year effect was not substantially different
306 from 0 in any year (Table S3); as a result, we did not include a random year effect in subsequent
307 models. We next incorporated a single environmental covariate into the linear AR(1) process
308 model based on our environmental covariate selection process (MinWaterTemp,
309 MinWaterTempLag, WaterTempMA, ΔSchmidt, SchmidtLag, WindDir, Precip, and GDD). The
310 influence of GDD was visibly non-linear in our preliminary analyses (Fig. S1) and thus, a
311 quadratic term was included in the model to evaluate GDD influence on *G. echinulata* growth.
312 We subsequently developed two-covariate models based on the performance of the
313 single-covariate models during the hindcasting validation period (Schmidt+Temp,
314 Schmidt+Precip, Temp+Precip, Precip+GDD). Finally, following observations that model
315 ensembles can provide more skilled predictions than a single model even when some ensemble
316 members are low-performing (Johansson et al. 2019), we generated a simple, unweighted model
317 ensemble to determine if it could out-perform our individual models (see Text S4 for model
318 ensemble details).
319

320 *Calibration using 2009-2014 data*

321 We calibrated each Bayesian state-space model to observed weekly data collected in
322 2009-2014 using the R packages *rjags* and *runjags* (*rjags* v.4-8, *runjags* v. 2.0.4-2, Denwood
323 and Plummer 2019, Plummer et al. 2019) in the R statistical environment (R version 4.0, R Core
324 Development Team, 2020). Models were structured as an annual loop for 20 weeks per year,
325 with each season extending from the last week in May to the first week in October. We natural
326 log-transformed *G. echinulata* densities and standardized all covariates using Z-scores to
327 facilitate model convergence. We ran three Markov chain Monte Carlo (MCMC) chains for each
328 model, with an adaptation period of 5,000 iterations, a burn-in of 10,000 iterations, and a sample
329 size of 50,000 iterations, which we thinned to 7,500 samples for hindcasting and model
330 assessment. We evaluated convergence using the potential scale reduction factor of the Gelman-
331 Rubin statistic, sometimes referred to as $\hat{R}$, where a value approaching 1 indicates that the model
332 has converged well on a parameter estimate both within and among MCMC chains (Table S4;
333 Table S5). Missing data occurred for several of our candidate environmental drivers, so NA
334 values were imputed using a missing data model with a Gaussian prior with mean and variance
335 of observations from the same week across the calibration period (2009-2014).

336

337 *Hindcasting validation using 2015-2016 data*

338 To validate our Bayesian state-space models, we conducted one-week-ahead and four-
339 week-ahead hindcasts of *G. echinulata* density in 2015-2016 using each of the fourteen models.
340 We assimilated data by iteratively adding one week of data to our model input dataset and re-
341 running our Bayesian models in *runjags* to update parameter calibrations and initial conditions.
342 The posterior output of each re-calibrated model was then used to produce hindcasts at one and

four weeks into the future. We hindcasted "future" driver data for each environmental covariate using data observations from 2009-2014 for the 2015 hindcasts and from 2009-2015 for the 2016 hindcasts. These historical driver timeseries were resampled with replacement for each of the 7,500 hindcast model iterations to account for week-to-week autocorrelation in driver data. As hindcasts were running, driver data from 2015-2016 were assimilated along with *G. echinulata* observations and thereby used to update posteriors throughout the hindcasting period.

Our primary criterion for hindcast model selection was based on predictive loss, calculated using the root mean square error (RMSE) of predictions and the variance of the predictive interval (defined in Table 1) via the following equation:

$$\text{Predictive loss} = \sqrt{RMSE^2 + predictive\ interval\ variance} \quad \text{eqn. 1}$$

The model with the smallest predictive loss at a particular forecast horizon indicates the best-performing model at that horizon (Gelfand and Ghosh 1998). We further compared models by subtracting the predictive loss of the best-performing model from the predictive loss of all other models to calculate change in predictive loss (ΔPL), with smaller ΔPL indicating better-performing models. We also calculated the standard deviation of the predictive interval (predictive S.D.), the percent of observations falling within the 95% predictive interval (coverage), the mean difference between median predicted and observed values (bias), and the difference in weeks between when maximum *G. echinulata* density was observed during the hindcasting period and when each model predicted maximum *G. echinulata* density (peak timing; Table 3).

Uncertainty partitioning of 2015-2016 hindcasts

We conducted uncertainty partitioning of our 2015-2016 cyanobacterial density hindcasts using a one-at-a-time ahead approach, where all sources of uncertainty were initially held at fixed values and then sequentially added back into the hindcasts. For example, all model parameter values were initially set to the mean of the posterior distribution of the calibrated model for all 7,500 hindcasting iterations; then, when we wanted to add parameter uncertainty to our hindcasts, we allowed parameter values to be drawn from the full posterior distribution, resulting in a variety of possible parameter values and subsequent estimation of uncertainty in those parameters. We added sources of uncertainty to our hindcasts in the following order: initial condition uncertainty, parameter uncertainty, driver data uncertainty, and process uncertainty. The order of uncertainties is important to specify as different sources of uncertainty can interact with each other. We were then able to calculate the relative contribution of each uncertainty source to total hindcast variance based on the incremental increase in variance as each source of uncertainty was added. Not all models included all the potential sources of uncertainty (e.g., the random walk model does not have driver data uncertainty because it does not include any environmental covariates).

Observation uncertainty is not included in our partitioning results because it does not propagate and therefore does not affect our uncertainty about the latent state of the system (Dietze 2017). However, to examine the relative importance of observation error in our study system, we assessed the estimated value of τ_{obs}, which is the precision ($\frac{1}{S.D.^2}$) of the normal distribution used to fit *G. echinulata* latent states to *G. echinulata* observations in the data model component of our Bayesian state-space models (Fig. 1). We also examined the increase in variance between our 95% credible interval (CI) and our 95% predictive interval (PI; CI and PI

are defined in Table 1).

All code used for data processing, model calibration and validation, uncertainty partitioning, and assessment of hindcast output are publicly available on the GLEON Github repository (https://github.com/GLEON/Bayes_forecast_WG/tree/eco_apps_release; DOI:10.5281/zenodo.3878781).

III. Results

Variability in G. echinulata abundance

Median *G. echinulata* density during the entire study period from 2009-2016 was 0.25 ± 8.2 colonies L^{-1} (median ± 1 S.D.; Fig. 4). During the model calibration period (2009-2014), *G. echinulata* density ranged from an annual maximum density of 1.2 colonies L^{-1} in 2012 to 81.6 colonies L^{-1} in 2013. Notably, while the calibration years included two periods of high *G. echinulata* density with visible surface scums (42.1 colonies L^{-1} in August 2010 and 81.4 colonies L^{-1} in September 2013), maximum density during the 2015-2016 hindcasting validation period was 14.1 colonies L^{-1} (Fig. 4). Temporal variability in environmental drivers of *G. echinulata* density included in state-space models is reported in Text S5 and Figures S2 – S9.

Models of G. echinulata growth

G. echinulata growth was dependent on *G. echinulata* density at the previous timestep, as indicated by a converged coefficient value ranging from 0.63 to 0.76 ± 0.06 to 0.10 for the AR(1) term across models (Table S4). Parameter estimates from calibrated models indicated that *G. echinulata* growth was positively associated with increases in water temperature, high

Schmidt stability, and a higher daily proportion of wind blowing towards the focal nearshore site (see Table S4; Table S5 for model coefficient values). The coefficient on the quadratic term for growing degree days based on water temperature (GDD) converged at -0.59 ± 0.17 (Table S5), indicating that increases in GDD at high values (i.e., late in the sampling season) were associated with decreasing *G. echinulata* growth.

Some variables that seemed promising based on our covariate selection protocol had estimated model coefficients close to 0 in calibrated state-space models (Precip, ΔSchmidt), indicating a limited effect on *G. echinulata* growth. The daily sum of precipitation (Precip) and weekly difference in median Schmidt stability (ΔSchmidt) model coefficients did not differ from zero (Table S5). Model coefficient values did not substantially change when environmental covariates were combined in two-covariate models (Schmidt+Temp, Schmidt+Precip, Temp+Precip, Precip+GDD, Table S5).

Environmental drivers no better than AR model at one-week-ahead hindcasts

All single and two-covariate models and the AR model had improved performance over the null RW model for one-week-ahead hindcasts based on predictive loss. Three models (AR, ΔSchmidt, and Precip) had a predictive loss of 2.25 ln(colonies L^{-1}) and were also comparable in terms of RMSE, coverage, and bias (Table 3; Fig. 5; models not shown in Fig. 5 can be found in Fig. S10, S11). Other environmental covariates that had non-zero model coefficients ($\widehat{\boldsymbol{\beta}}$ parameters; Table S5), such as the water temperature covariates, SchmidtLag, and WindDir, were not good predictors of *G. echinulata* densities at the one-week horizon (Table 3).

No model correctly predicted the week or magnitude of peak *G. echinulata* density for the 2015-2016 hindcasting period (10 September 2015) at the one-week horizon; however, the

best-performing AR model was able to predict when peak density occurred with only a one week lag after the observed peak (Table 3).

Water temperature models more skilled than AR at four-week forecast horizon

Models containing water temperature covariates out-performed the AR model at the four-week horizon (Table 3; Fig. 6; models not shown in Fig. 6 may be found in Fig. S12, S13). The three best-performing models at the four-week horizon were MinWaterTempLag, WaterTempMA, and Schmidt+Temp, all with a predictive loss of 2.42 ln(colonies L^{-1}). Other models containing water temperature covariates (MinWaterTemp, GDD, Temp+Precip, Precip+GDD) also performed relatively well at the four-week horizon, all with $\Delta PL = 0.01$ ln(colonies L^{-1}). Models containing water temperature covariates tended to have lower bias and lower predictive S.D. than other models at the four-week horizon; however, the reduction in predictive S.D. corresponded to a loss in coverage (Table 3).

Despite the improvement of water temperature models over the AR model, no examined model successfully predicted the timing of peak *G. echinulata* density at the four-week horizon, and all models missed the peak by 12 or 14 weeks. Given the structure of our models (seasonal for-loop), this means that models missed the 10 September 2015 peak altogether (Fig. 6).

The unweighted model ensemble was not among the top-performing models at either the one-week or four-week forecast horizon, with a ΔPL of 0.05 ln(colonies L^{-1}) at the one-week horizon and 0.09 ln(colonies L^{-1}) at the four-week horizon (Table 3; Text S4).

Process uncertainty dominates hindcast credible intervals

Process uncertainty represented the largest proportion of uncertainty in the credible interval for all models. The proportion of the variance attributed to process uncertainty increased with hindcast horizon, largely due to a reduction in initial conditions uncertainty (Fig. 7; models not shown in Fig. 7 can be found in Fig. S14). Neither increases in model structural complexity or differences in model covariates substantially decreased the proportional contribution of process uncertainty (Fig. 8). The mean contribution of process uncertainty across the hindcasting period ranged from 73% of hindcast uncertainty in the RW model to 81% in the MinWaterTempLag model for one-week-ahead hindcasts, and from 83% in the SchmidtLag model to 93% in the AR model for four-week-ahead hindcasts. However, the relative contribution of process uncertainty to total hindcast uncertainty did vary across the hindcasting period for individual models (mean, minimum, and maximum contributions of all uncertainty sources during 2015-2016 can be found in Tables S6-S7). Excluding the RW and AR models, whose credible intervals became almost completely comprised of process error as the forecast horizon progressed, process error was sometimes as low as 54% (ΔSchmidt, SchmidtLag, WindDir) or as high as 96% (ΔSchmidt, Precip) for one-week-ahead hindcasts, and as low as 73% (SchmidtMaxLag) or as high as 95% (Precip) for four-week-ahead hindcasts.

The second largest component of uncertainty in hindcasts was due to initial conditions estimation, although this source of uncertainty quickly declined to negligible levels by the four-week-ahead forecast horizon for all models (Fig. 7; Fig. 8). Averaged across the hindcasting period, initial conditions uncertainty contributed from 13% (MinWaterTempLag; Schmidt+Temp) to 27% (RW) of the uncertainty for one-week-ahead hindcasts but comprised only from 1 % to 9% of total uncertainty for four-week ahead hindcasts. Initial conditions

uncertainty was largest (30-43% of total uncertainty) for one-week-ahead hindcasts following a week with a missing *G. echinulata* observation (Fig. S15a).

Parameter and driver error had negligible contributions to total hindcast uncertainty for both one-week-ahead and four-week-ahead hindcasts (Fig. 7; Fig. 8; Fig. S14 and Tables in Supplemental Material).

Observation uncertainty in 95% PI

Observation uncertainty was a substantial component of uncertainty for all models and τ_{obs} ranged from 1.72 to 1.89 ± 0.35 to 0.38 ln(colonies L^{-1})$^{-2}$ across models. This corresponds to a standard deviation of ~0.75 ln(colonies L^{-1}) or ~2.1 colonies L^{-1}, which is large considering that median *G. echinulata* density during the hindcasting period was 0.56 ± 2.9 colonies L^{-1}. These relatively large estimates of observation uncertainty contributed to an average increase of 0.94 ln(colonies L^{-1}) in the 95% predictive interval (PI) over the 95% credible interval (CI; mean range 4.88 ± 0.40 ln(colonies L^{-1})) across all models for one-week-ahead hindcasts (Fig. 5). The difference in PI was higher for the four-week-ahead hindcasts, with a 1.16 ln(colonies L^{-1}) increase over the 95% CI (mean CI range 5.61 ± 1.11 ln(colonies L^{-1})) across all models (Fig. 6). Again considering the relatively low density of *G. echinulata* during our hindcasting period, these 95% PI – 95% CI range differences translate to a large contribution of observation uncertainty to predicted *G. echinulata* densities (95% PI – 95% CI range differences of 2.56 colonies L^{-1} at the one-week horizon and 3.12 colonies L^{-1} at the four-week horizon).

IV. Discussion

Understanding ecological systems to better forecast future events is a critical challenge for managing resources and public health. Use of standardized ecological forecasting approaches provides a much-needed framework for prioritizing research efforts to meet this challenge. While there are numerous hypotheses and studies linking environmental drivers to the *G. echinulata* surface scums that challenge water quality management in oligotrophic lakes (e.g., Roelofs and Oglesby 1970, Istvánovics et al. 1993, Hyenstrand et al. 2000, Karlsson-Elfgren et al. 2005, Carey et al. 2014, Napiórkowska-Krzebietke and Hutorowicz 2015), few have fully evaluated the predictive influence of these environmental variables. We calibrated models to evaluate how well environmental variables that had previously been associated with cyanobacterial density explain changes in density over near-term timescales and evaluated each model for forecast skill. We demonstrate that significant explanatory variables in calibration or best-fit models are not necessarily effective driver variables in near-term ecological forecasts, and that driver variables that may adequately capture low densities may not successfully predict rare high-density events. The dominance of process and initial conditions uncertainty in our forecasts emphasizes that *G. echinulata* densities are likely a product of both growth and movement of colonies, that spatial and temporal misalignment of driver data and density observations are ongoing challenges in this forecasting system, and that imperfect observation of both *G. echinulata* density and environmental covariates substantially affect forecast skill.

Of all the environmental covariates we examined, water temperature metrics were important in both calibration and hindcast models and may be a promising suite of drivers for predicting *G. echinulata* density. Both lagged and moving average measures of water temperature (MinWaterTempLag, WaterTempMA) were positively associated with changes in

G. echinulata density and more skilled than the baseline AR model in hindcasting *G. echinulata* density at the four-week horizon. This is consistent with studies demonstrating that cyanobacteria benefit from warmer temperatures (e.g., Paerl and Huisman 2008, Carey et al. 2012b), that water temperature is a good predictor of cyanobacterial density (Rousso et al. 2020), and that antecedent conditions can affect cyanobacterial growth and phytoplankton community structure (Bormans et al. 2005, Madgwick et al. 2006). Our results further suggest that a minimum water temperature predictor (MinWaterTempLag) may be useful for forecasting *G. echinulata* density, which agrees with findings from a previous study examining predictors of *Lyngbya majuscula* blooms in an Australian bay (Hamilton et al. 2009). However, we were unable to identify any environmental covariates that improved *G. echinulata* density predictions over the AR model at the one-week horizon, suggesting that water temperature is likely not adequate to forecast cyanobacterial densities at this time scale.

Process uncertainty dominated hindcast uncertainty across all models. Neither increases in model structural complexity nor differences in model covariates substantially decreased the proportional contribution of process uncertainty to forecast uncertainty. The predominance of process uncertainty, coupled with low parameter uncertainty (Fig. 8), indicates a substantial need for research to better understand how and why *G. echinulata* densities change. Some of the environmental covariates we explored may sufficiently explain weekly differences in frequently-observed low densities but none of the models we calibrated had skill at forecasting peak abundances, which appeared and declined suddenly. In theory, it is possible that *G. echinulata* dynamics are dominated by stochasticity (e.g., Carpenter et al. 2020), in which case improvement to model structure would not effectively reduce process uncertainty. However, our results suggest that a process model more aligned with the biology of the focal cyanobacterium,

as well as more frequent sampling events, could be promising avenues for model development to reduce process uncertainty and improve forecast skill.

The low-frequency surface scum events in Lake Sunapee likely result from the compound effects of cyanobacterial population growth in the water column, recruitment of dormant cells from the sediments, movement of colonies within the lake, and accumulation on the lake surface (Roelofs and Oglesby 1970, Karlsson-Elfgren et al. 2005, Carey et al. 2014, Cyr 2017). Each of these may be best predicted by different drivers at different temporal or spatial scales, and many more years of data are likely needed to identify significant predictors of these low-frequency, high-density cyanobacterial growth events. Absent the possibility of data-driven models to predict low-frequency events, more mechanistic process structure in the forecasting model is needed. Changes in the relative importance of driver and process uncertainty in our hindcasts may elucidate when during the season currently unaccounted-for ecological processes are important and how we could better align environmental driver and *G. echinulata* density sampling in future studies. For example, one of the best-performing models at the four-week horizon (MinWaterTempLag) exhibited low driver uncertainty but high process uncertainty during the last five weeks of the 2015 sampling season (Fig. S16). This suggests that *G. echinulata* were responding to variables other than water temperature and a careful examination of other environmental conditions during this period could illuminate additional ecological processes that should be included in forecasting models. Further, incorporating more mechanistic representations of explanatory variables that were significant during model calibration but not skilled at forecasting, such as wind direction and thermal stratification (SchmidtLag), might help constrain process uncertainty. Models including both temperature-dependent growth rate equations and a process representation of the effect of thermal stratification on surface scum

formation or of colony transport via wind-driven mixing (e.g., Wallace et al. 2000, Ndong et al. 2017, Cyr 2017) might generate better forecasts. A more complex mechanistic model could also include additional life history stages of *G. echinulata* beyond vegetative growth in the water column. For example, it is well-documented that recruitment from the sediments to the pelagic zone is an important life stage for *G. echinulata*, potentially contributing 4-40% of the water column population each week (e.g., Barbiero and Welch 1992, Carey et al. 2014b).

While the contribution of driver data uncertainty (accuracy of driver measurements and forecasts) to our hindcasts was small, spatial mismatches between driver data and response variable data may also contribute to process uncertainty. Thus, the inclusion of more nearshore site variables, rather than variables collected in the deep-water pelagic zone, might reduce process uncertainty by better characterizing the effect of environmental drivers on localized nearshore processes. For example, we did not consider nearshore nutrient concentrations. *G. echinulata* can both fix nitrogen and sequester excess phosphorus in the sediments before recruiting to the water column, thereby providing its own nutrients for pelagic growth (Barbiero and Welch 1992, Cottingham et al. 2015); moreover, our study lake has very low nitrogen and phosphorus concentrations. However, it is possible that nearshore nutrient concentrations could have an effect on *G. echinulata* growth. In addition, local site variables have been found important in driving benthic recruitment (Carey et al. 2014), so inclusion of more nearshore drivers could be a complementary approach to including benthic recruitment in models.

Forecast skill in this system could also be improved by refining our estimates of initial conditions. In particular, both total hindcast variance and the proportional contribution of initial condition uncertainty exhibited large increases immediately after missing *G. echinulata* density observations, and this increase perpetuated through the four-week horizon (Fig. S11). This

suggests that increasing the spatial or temporal frequency of observations could improve forecast skill (e.g., Fox et al. 2018), as cyanobacterial densities can be spatially heterogeneous (Franks 1997, Serizawa et al. 2008, Wynne and Stumpf 2015) and change quickly on short timescales (Dokulil and Teubner 2000, Huisman and Hulot 2005, Rolland et al. 2013). Because sampling and counting *G. echinulata* is labor-intensive, increasing observational frequency might necessitate assimilating other measures of cyanobacterial abundance into forecasts, such as fluorescence-based biomass measurements (e.g., Catherine et al. 2012) and spectrophotometric pigment analysis (e.g., Küpper et al. 2007, Thrane et al. 2015). Furthermore, as phytoplankton counts are notoriously variable (Rott et al. 2007, Vuorio et al. 2007), increased spatio-temporal sampling frequency and incorporation of measures of cyanobacterial abundance besides counts might constrain the high observation uncertainty in *G. echinulata* density data, thereby improving comparisons of models to data. However, before investing in costly increased *in-situ* monitoring, the potential benefit of increased sampling effort could be determined through simulated data experiments exploring how different sampling techniques and frequencies affect forecast precision (following Dietze 2017a).

Our uncertainty partitioning results from oligotrophic lake cyanobacterial density hindcasts have some commonalities with other uncertainty partitioning efforts, contributing insight into the dominant sources of uncertainty across near-term forecasts in ecological systems. Our hindcasts were dominated by process uncertainty and emphasize the need for research to better understand the ecology of phytoplankton density changes in nutrient-poor systems. Similar results have been reported for ecological forecasts at decadal and multi-decadal timescales predicting variables ranging from forest biomass and productivity (Thomas et al. 2018) to vertebrate species distributions (Diniz-Filho et al. 2009, Watling et al. 2015). In addition, our

finding that initial conditions uncertainty is an important contributor to forecast uncertainty is consistent with terrestrial carbon forecasts at the annual scale (Fox et al. 2018) and lake chlorophyll-*a* forecasts at the weekly scale (Huang et al. 2013). However, several other aquatic and terrestrial forecasts that could leverage good process understanding found that driver data uncertainty dominated ecological forecasts (e.g., Mbogga et al. 2010, Dietze 2017b, Ouellet-Proulx et al. 2017, Jiang et al. 2018, Thomas et al. 2020). Across ecosystems, a skillful process model and correspondingly low process uncertainty are likely prerequisites for other forms of uncertainty, such as driver data uncertainty, to dominate.

Developing forecasts for low-frequency events, like cyanobacterial growth events, is especially challenging and uncertainty partitioning in these highly dynamic systems can help prioritize research to improve process understanding or increase sampling frequency in space or time. Standardized and formal uncertainty partitioning across studies and ecosystems could identify consistent or contrasting patterns in forecast skill at different horizons in ecosystems where low-frequency or rare events have significant consequences, such as cyanobacterial blooms (Kim et al. 2014) and insect (Hobbs et al. 2015) and disease outbreaks (Grünwald et al. 2000). Overall, despite considering dozens of possible environmental covariates, our hindcasts were not skilled enough to predict the sudden, infrequent increases in cyanobacterial density that cause concern for water resource managers and other stakeholders in both oligotrophic and eutrophic lakes. However, formal uncertainty partitioning provided insight on how to target data collection and modeling efforts, following Dietze et al. (2018). Even if our initial forecasting efforts are not very skilled, the process of iteratively confronting our models with data and quantitatively examining forecast uncertainty teaches us how to improve (Bauer et al. 2015). Access to data and standardized expectations for uncertainty partitioning are critical to the

iterative improvement of forecast skill. Our study was enabled both by collaborative sharing of long-term data through the Global Lake Ecological Observatory Network, which facilitated calibration and validation of hindcasting models over many years (Cottingham et al. 2020a, 2020b, LSPA et al. 2020a, 2020b), and access to publicly available R code examples of how to conduct uncertainty partitioning (https://github.com/EcoForecast/EF_Activities). As such, our study illustrates the importance of open science and findable, accessible, interoperable, and reusable (FAIR) scientific practices with respect to data and code (Wilkinson et al. 2016, Powers and Hampton 2019) to reduce barriers to adoption of techniques such as uncertainty partitioning and advance the field of ecological forecasting.

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Tables

Table 1: Terms associated with partitioning uncertainty in ecological models and forecasts. Definitions are adapted from Dietze (2017a) unless otherwise specified.

Term	Definition	Example
Credible interval	Interval within which a parameter or model prediction falls with a specified probability; does not include observation uncertainty	95% interval of possible latent values of chorophyll-*a* forecasted for tomorrow, incorporating initial conditions, process, parameter, and driver data uncertainty
Driver data uncertainty	Uncertainty arising from observation uncertainty in the estimate or measurement of driver data (environmental predictors of the forecasted state)	Uncertainty in observations of soil temperature needed to drive a soil respiration model; uncertainty in weather forecasts
Hindcast	Predictions of a past time period with specified uncertainty using data (withheld from model calibration) that are iteratively assimilated into the model (Jolliffe and Stephenson 2003)	Making model predictions for tick abundances observed two years ago using a model calibrated to observations from ten years prior.
Initial conditions uncertainty	Uncertainty associated with the starting conditions of a forecasting model run	Uncertainty in initial focal states, such as fish abundance, chlorophyll-a, or soil carbon stock
Observation uncertainty	Difference between the observed data and the true (latent) state that the model is designed to predict; does not propagate forward, so it does not affect the credible interval.	Calibration uncertainty in a temperature sensor; sampling uncertainty when estimating species abundance
Parameter uncertainty	Variance around the model parameter estimates	Uncertainty in the growth rate parameter in a timber yield model
Predictive interval	Interval within which predicted observations are expected to fall with a specified probability; includes observation uncertainty; should be used when comparing models to observed data	95% interval of possible observations of chorophyll-*a* forecasted for tomorrow
Process uncertainty	Uncertainty due to model specification (ecological processes that are simplified, absent, or incorrectly represented by the model) or inherent stochasticity in the system	Uncertainty arising from not including an important life history stage in a population growth model; uncertainty arising from demographic stochasticity in plankton communities
Random effects uncertainty	Uncertainty associated with estimation of random effects, which are used to describe shared variance across groups in space and time	Uncertainty in the value of a random site effect in a metacommunity model including many different sampling sites

Table 2: List of Bayesian state-space models and covariates. m_t is the latent state of *G. echinulata* density at time *t*, *N()* represents a normal distribution with mean and precision (τ_{proc}). *x*, *x1* and *x2* are environmental covariates in single-covariate and two-covariate models. $\boldsymbol{\beta}$ represents parameters for the process model equations.

Model name	Model description	Process model	Covariates
RW	Random walk	$m_{t+1} = N(m_t, \tau_{proc})$	
AR	Autoregressive with one lag (AR(1))	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t), \tau_{proc}\right)$	
MinWaterTemp	AR(1) with a single linear covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x_{t+1}), \tau_{proc}\right)$	minimum water temperature on sampling day
MinWaterTempLag	AR(1) with a single linear covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x_t), \tau_{proc}\right)$	minimum water temperature 1 week prior to the sampling day
WaterTempMA	AR(1) with a single linear covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x_t), \tau_{proc}\right)$	seven-day moving average of water temperature including the sampling day
ΔSchmidt	AR(1) with a single linear covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * (x_{t+1} - x_t)), \tau_{proc}\right)$	difference in median Schmidt stability between 1 week prior to the sampling day and the sampling day
SchmidtLag	AR(1) with a single linear covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x_t), \tau_{proc}\right)$	maximum Schmidt stability 1 week prior to sthe sampling day
WindDir	AR(1) with a single linear covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x_t), \tau_{proc}\right)$	proportion of daily wind measurements blowing towards Site 1 with a two-day lag
Precip	AR(1) with a single linear covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x_t), \tau_{proc}\right)$	sum of daily precipitation on the sampling day
GDD	AR(1) with a single quadratic covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x_t + \beta_3 * x_t^2), \tau_{proc}\right)$	growing degree days
Schmidt+Temp	AR(1) with two linear covariates	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x1_t + \beta_3 * x2_t), \tau_{proc}\right)$	difference in median Schmidt stability between 1 week prior the sampling day and the sampling day and seven-day moving average of water temperature including the sampling day
Schmidt+Precip	AR(1) with two linear covariates	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x1_t + \beta_3 * x2_t), \tau_{proc}\right)$	difference in median Schmidt stability between the previous sampling day and the day of sampling and sum of daily precipitation on the sampling day
Temp+Precip	AR(1) with two linear covariates	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x1_t + \beta_3 * x2_t), \tau_{proc}\right)$	seven-day moving average of water temperature including the sampling day and sum of daily precipitation on the sampling day
Precip+GDD	AR(1) with one linear and one quadratic covariate	$m_{t+1} = N\left((\beta_0 + \beta_1 * m_t + \beta_2 * x1_t + \beta_3 * x2_t + \beta_4 * x2_t^2), \tau_{proc}\right)$	sum of daily precipitation on the sampling day and growing degree days

Table 3: Hindcasting results across models for the 2015-2016 hindcasting period. RMSE = root mean square error; Predictive variance = mean variance of the predictive interval; Predictive loss = $\sqrt{RMSE^2 + predictive\ variance}$; Δ Predictive loss = the difference between predictive loss for each model and the best-performing model for that forecast horizon; Coverage = the percent of observations falling within the 95% predictive interval; Peak timing = the number of weeks between peak *G. echinulata* density during the hindcasting period and when the model predicted peak density; Bias = mean difference between median predicted and observed values. Note that all assessment metrics are conducted on log-transformed data except for mean bias. *best-performing models at either the one-week or four-week forecast horizon based on evaluation of Δ Predictive loss.

	RMSE *natural log colonies L^{-1}*		**Predictive S.D.** *natural log colonies L^{-2}*		**Predictive loss** *natural log colonies L^{-2}*		**Δ Predictive loss (ΔPL)** *natural log colonies L^{-2}*		**Coverage** *%*		**Peak timing** *weeks*		**Bias** *colonies L^{-1}*	
Model name	1 wk	4 wk	1 wk	4 wk	1 wk	4 wk	1 wk	4 wk	1 wk	4 wk	1 wk	4 wk	1 wk	4 wk
RW	1.89	2.23	1.63	2.98	2.5	3.72	0.25	1.3	97.2	100	1	14	-0.41	-0.96
AR*	1.67	1.61	1.51	2.08	2.25	2.63	0	0.21	97.2	100	1	14	-0.92	-1.52
MinWaterTemp	1.82	1.59	1.43	1.83	2.31	2.43	0.06	0.01	94.4	93.5	14	12	-0.93	-1.41
MinWaterTempLag*	1.79	1.62	1.45	1.79	2.3	2.42	0.05	0	91.7	87.1	14	12	-1	-1.45
WaterTempMA*	1.78	1.59	1.45	1.83	2.3	2.42	0.05	0	94.4	93.5	14	12	-0.95	-1.42
ΔSchmidt*	1.66	1.62	1.52	2.08	2.25	2.63	0	0.21	94.4	100	1	14	-0.91	-1.52
SchmidtLag	1.75	1.58	1.46	2.04	2.28	2.58	0.03	0.16	97.2	100	14	14	-0.9	-1.41
WindDir	1.78	1.55	1.5	2	2.33	2.53	0.08	0.11	94.4	100	1	14	-0.96	-1.51
Precip*	1.66	1.62	1.52	2.09	2.25	2.64	0	0.22	94.4	100	1	14	-0.92	-1.51
GDD	1.84	1.59	1.43	1.84	2.33	2.43	0.08	0.01	94.4	96.8	14	12	-1.08	-1.41
Schmidt+Temp*	1.79	1.61	1.46	1.81	2.31	2.42	0.06	0	91.7	87.1	14	14	-0.97	-1.44
Schmidt+Precip	1.66	1.62	1.53	2.08	2.26	2.64	0.01	0.22	97.2	100	1	14	-0.92	-1.52
Temp+Precip	1.78	1.61	1.46	1.83	2.3	2.43	0.05	0.01	94.4	93.5	14	12	-0.96	-1.43
Precip+GDD	1.81	1.59	1.44	1.84	2.31	2.43	0.06	0.01	97.2	96.8	14	14	-0.88	-1.31
Ensemble	1.76	1.55	1.49	1.97	2.3	2.51	0.05	0.09	97.2	100	14	14	-0.96	-1.48

Figure legends

Figure 1: Conceptual figure of a Bayesian state-space model, where y_t is the observed cyanobacterial density at time t, x_t are driver data (environmental covariates) at time t, m_t is the estimated true, or latent, cyanobacterial density at time t, $\boldsymbol{\beta}$ is a vector of parameters in the process model (slope, intercept, etc.), and τ_{proc} and τ_{obs} are the precisions of normal distributions representing process error and observation error, respectively. Parameters (rounded-edge rectangle) are modeled as distributions in the parameter model. Parameters, along with driver data, determine the predicted latent states (ovals; also modeled as a distributions) in the process model, which are fitted to observations using the data model.

Figure 2: Map of Lake Sunapee, New Hampshire, USA with locator map (inset). Data from Site 1 were used for Bayesian state-space models, data from Site 2 were used to inform priors for Site 1 models, and data from Site 3 provided lake-level covariates for Site 1 models.

Figure 3: Model development workflow diagram. Model equations and descriptions of covariates included in each model can be found in Table 2.

Figure 4: Timeseries of *G. echinulata* density at Site 1 in Lake Sunapee from 2009-2016 (a, c); panels b) and d) show a reduced scale to better illustrate variability at low density.

Figure 5: Timeseries of median predicted and observed *G. echinulata* density for one-week-ahead hindcasts in 2015 for the best-performing models (b-g; Table 3), as well as the RW null model (a). Similar figures for 2016 hindcasts and models not shown here may be in found in the supplemental material (Fig. S10, S11).

Figure 6: Timeseries of median predicted and observed *G. echinulata* density for four-week-ahead hindcasts in 2015 for the best-performing models (b-g; Table 3), as well as the RW null model (a). Similar figures for 2016 hindcasts and models not shown here may be in found in the

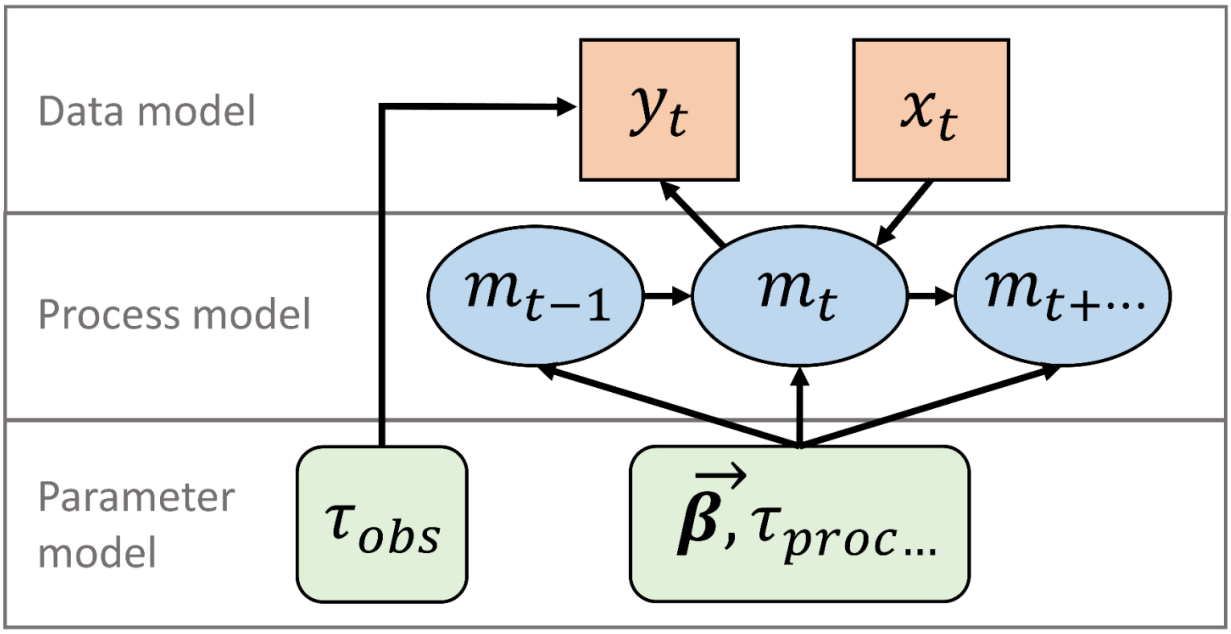
supplemental material (Fig. S12, S13). Note the y-axis change between Figures 5 and 6 to accommodate larger credible and predictive intervals at the four-week forecast horizon.

Figure 7: Uncertainty partitioning of the one-week-ahead to four-week-ahead credible interval for hindcasts averaged across the 2015-2016 hindcasting period for the best-performing models (b-g; Table 3), as well as the RW null model (a). Similar figures for other models may be found in the supplemental material (Fig. S14).

Figure 8: Uncertainty partitioning for a) one-week-ahead and b) four-week-ahead hindcasts averaged across the 2015-2016 hindcasting period across models. White triangles indicate a best-performing model at the respective forecast horizon as assessed by Δ Predictive loss (Table 3).

Figures

Figure 1



1066 **Figure 2**

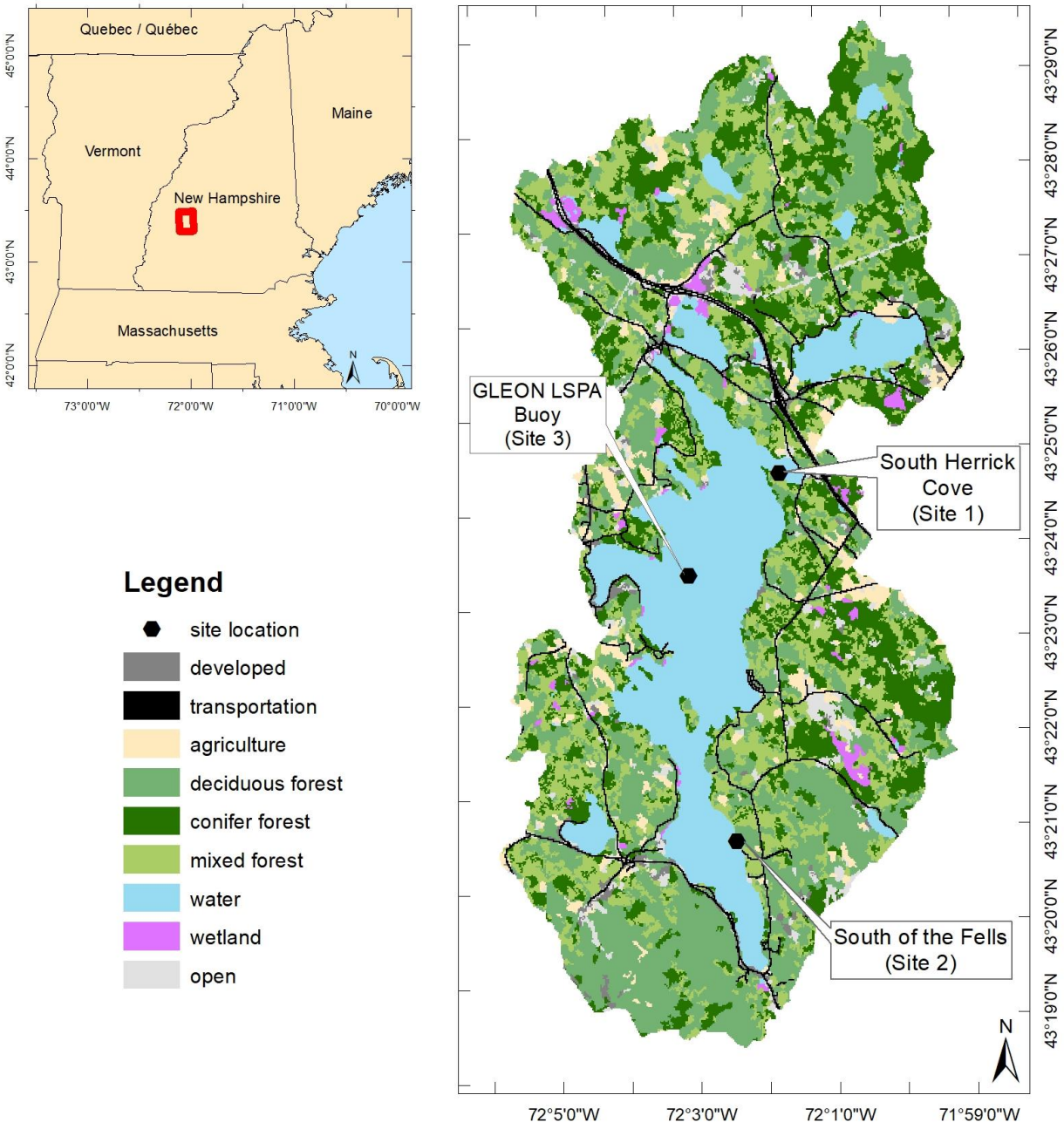


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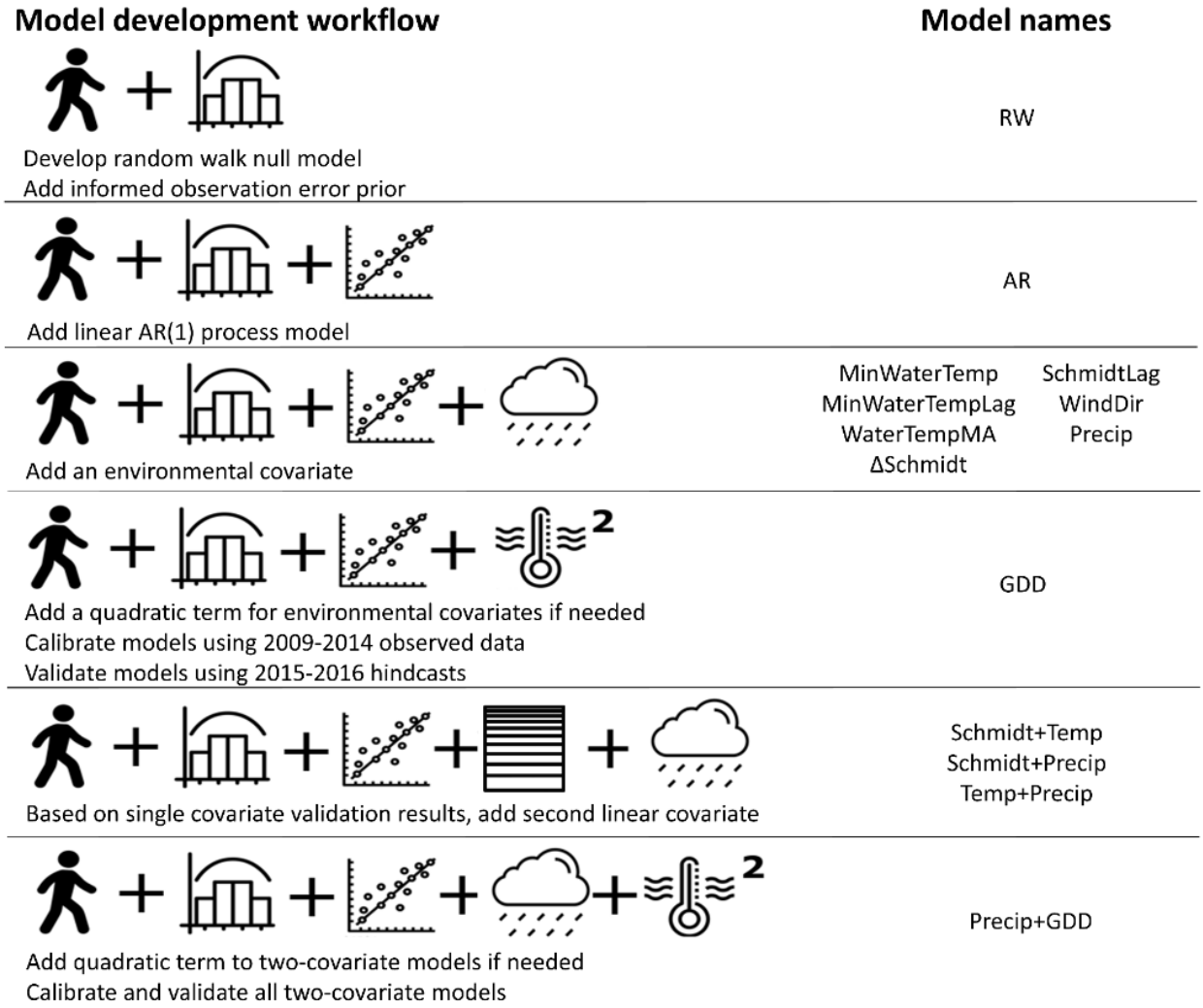
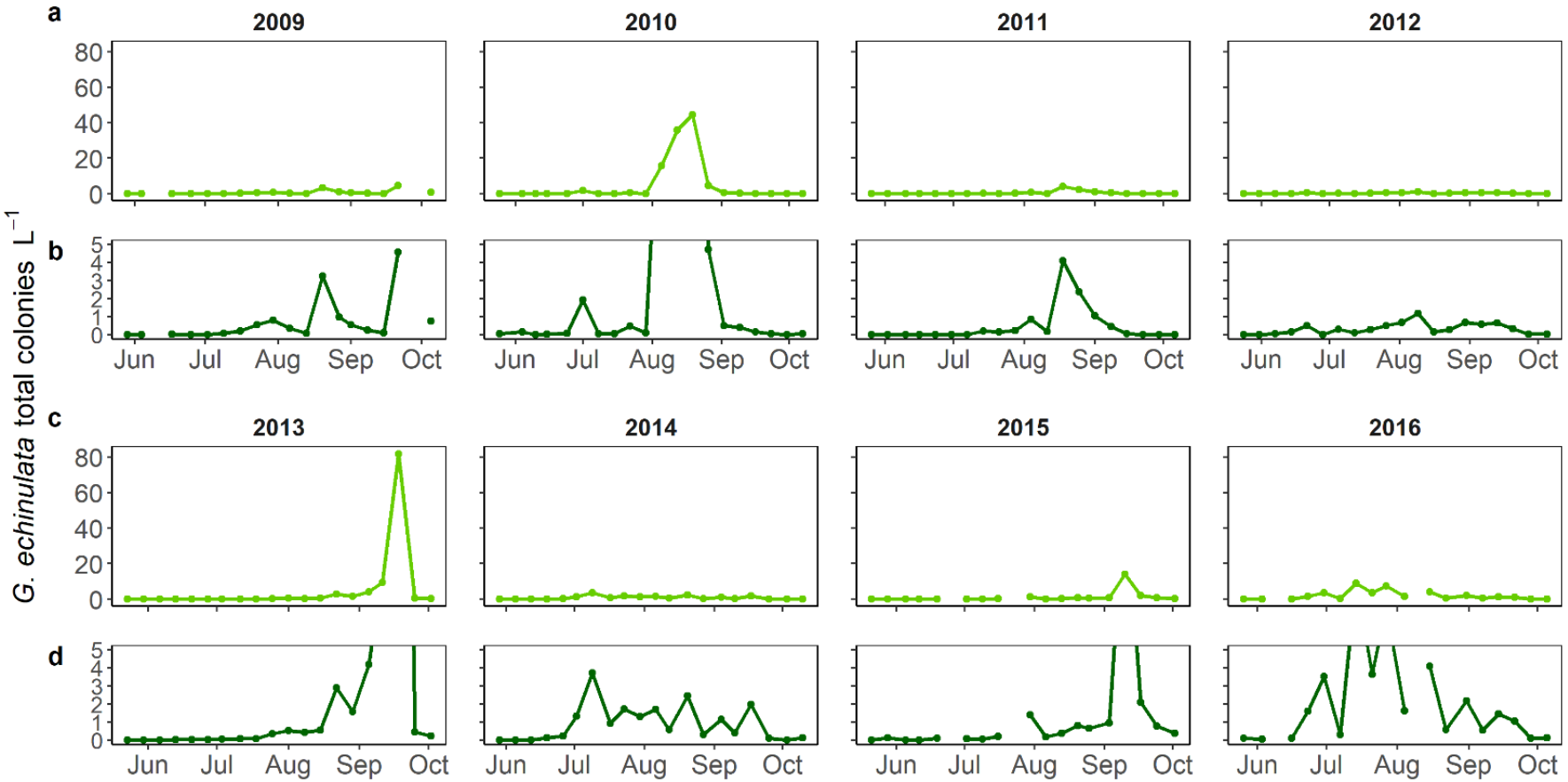
Figure 3


Model development workflow
Model names
Develop random walk null model
Add informed observation error prior
RW
Add linear AR(1) process model
AR
Add an environmental covariate
MinWaterTemp
MinWaterTempLag
WaterTempMA
ΔSchmidt
SchmidtLag
WindDir
Precip
Add a quadratic term for environmental covariates if needed
Calibrate models using 2009-2014 observed data
Validate models using 2015-2016 hindcasts
GDD
Based on single covariate validation results, add second linear covariate
Schmidt+Temp
Schmidt+Precip
Temp+Precip
Add quadratic term to two-covariate models if needed
Calibrate and validate all two-covariate models
Precip+GDD

1082 **Figure 4**



1083

Figure 5

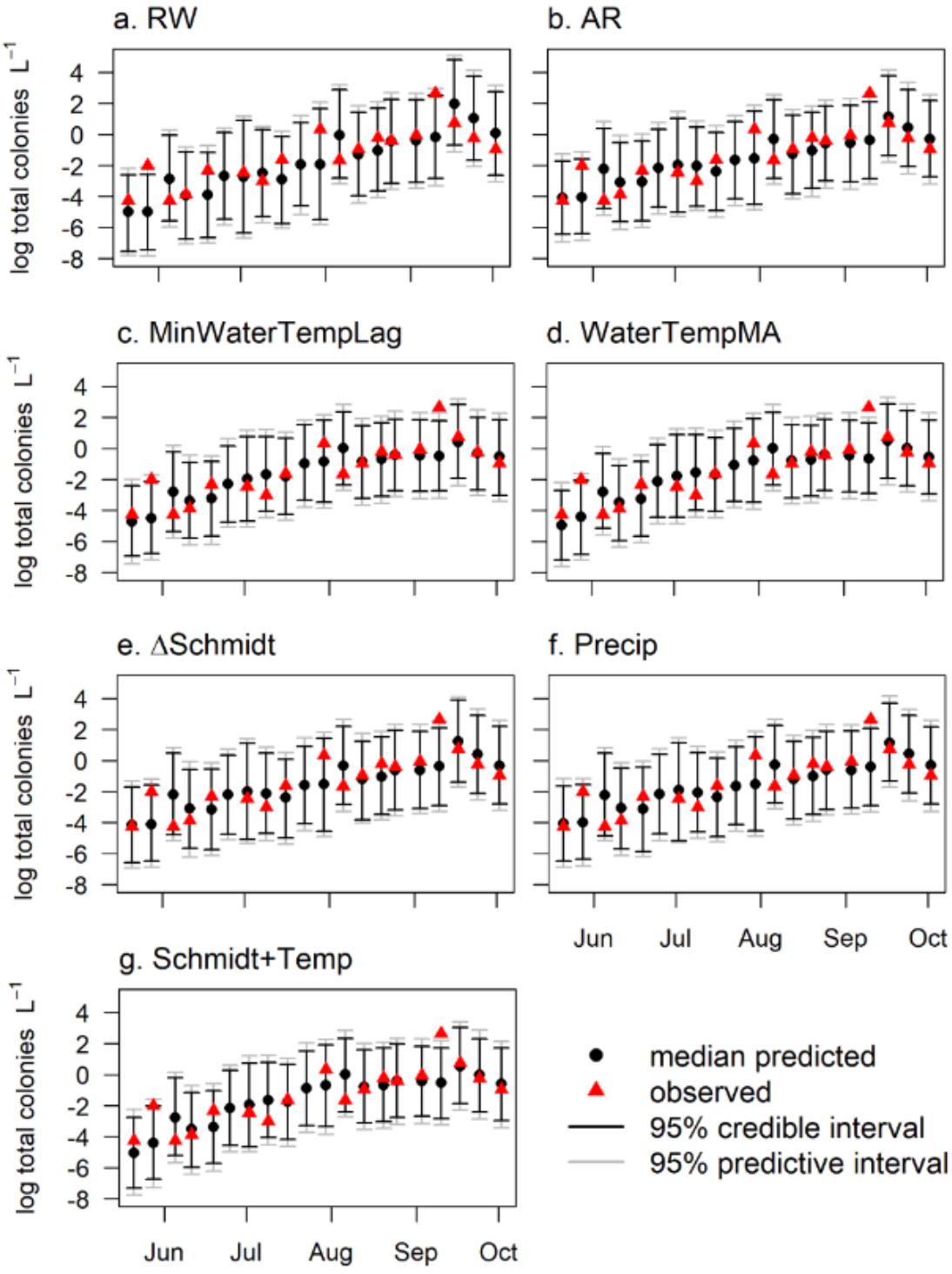

a. RW
b. AR
c. MinWaterTempLag
d. WaterTempMA
e. ΔSchmidt
f. Precip
g. Schmidt+Temp
log total colonies L⁻¹
4
2
0
-2
-4
-6
-8
Jun
Jul
Aug
Sep
Oct
median predicted
observed
95% credible interval
95% predictive interval

Figure 6

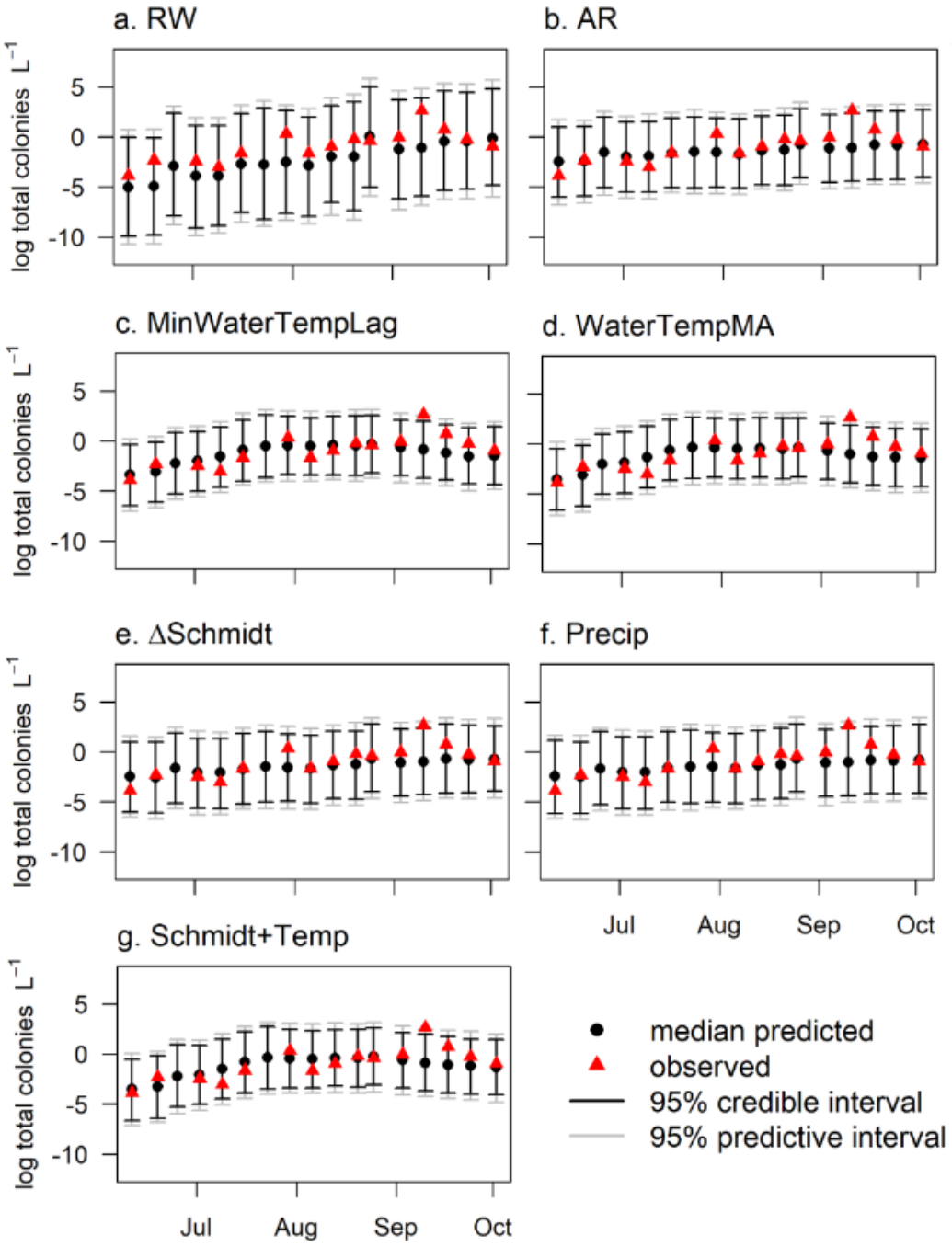

a. RW
b. AR
c. MinWaterTempLag
d. WaterTempMA
e. ΔSchmidt
f. Precip
g. Schmidt+Temp
log total colonies L⁻¹
5
0
-5
-10
Jul
Aug
Sep
Oct
median predicted
observed
95% credible interval
95% predictive interval

Figure 7

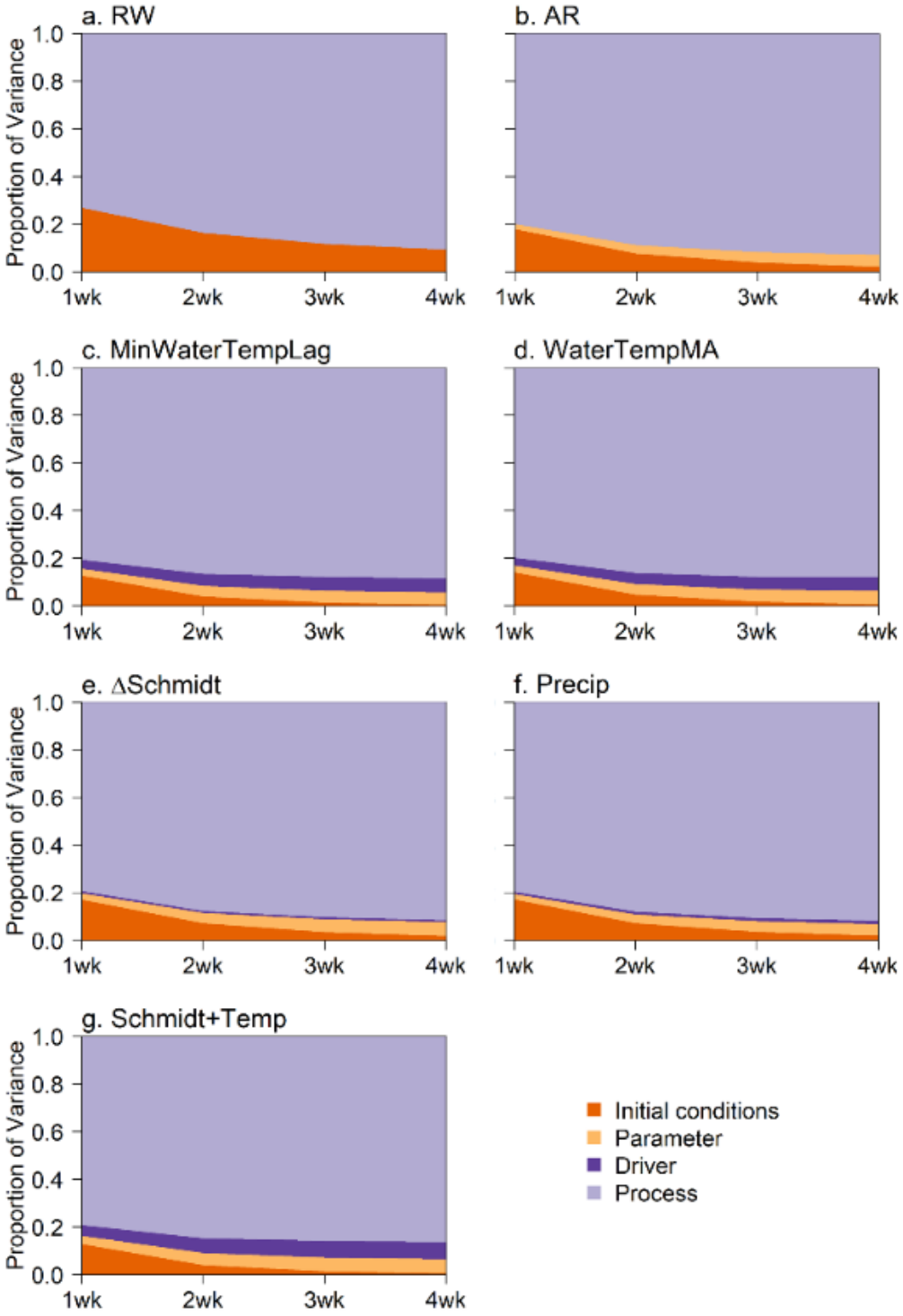
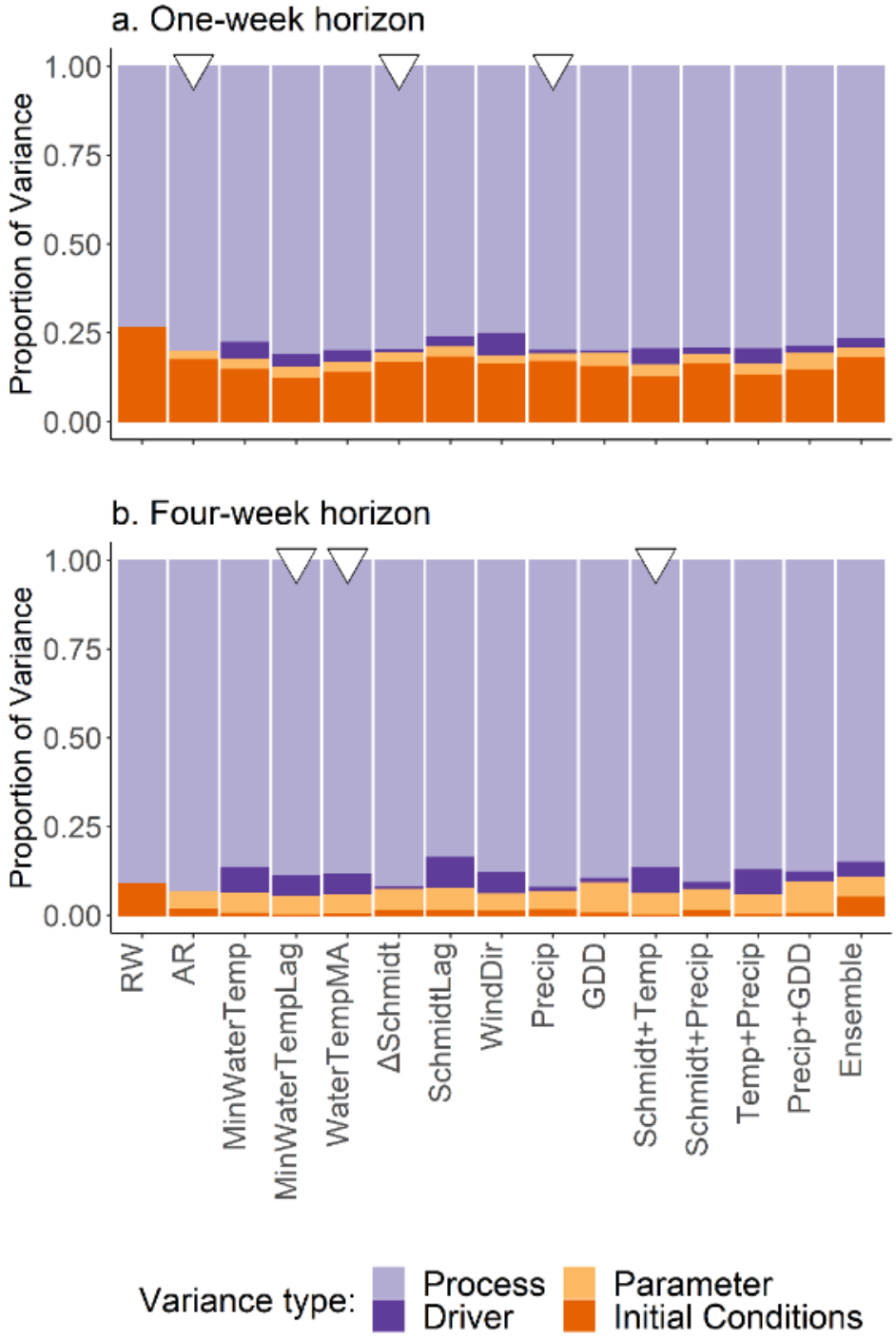

a. RW
b. AR
c. MinWaterTempLag
d. WaterTempMA
e. ΔSchmidt
f. Precip
g. Schmidt+Temp
Proportion of Variance
0.0
0.2
0.4
0.6
0.8
1.0
1wk
2wk
3wk
4wk
Initial conditions
Parameter
Driver
Process

Figure 8


a. One-week horizon
b. Four-week horizon
Proportion of Variance
1.00
0.75
0.50
0.25
0.00
RW
AR
MinWaterTemp
MinWaterTempLag
WaterTempMA
ΔSchmidt
SchmidtLag
WindDir
Precip
GDD
Schmidt+Temp
Schmidt+Precip
Temp+Precip
Precip+GDD
Ensemble
Variance type:
Process
Driver
Parameter
Initial Conditions