Bayesian model averaging for harmful algal bloom prediction

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Abstract. Harmful algal blooms (HABs) are a worldwide problem that have been increasing in frequency and extent over the past several decades. HABs severely damage aquatic ecosystems by destroying benthic habitat, reducing invertebrate and fish populations, and affecting larger species such as dugong that rely on seagrasses for food. Few statistical models for predicting HAB occurrences have been developed, and in common with most predictive models in ecology, those that have been developed do not fully account for uncertainties in parameters and model structure. This makes management decisions based on these predictions more risky than might be supposed. We used a probit time series model and Bayesian model averaging (BMA) to predict occurrences of blooms of *Lyngbya majuscula*, a toxic cyanophyte, in Deception Bay, Queensland, Australia. We found a suite of useful predictors for HAB occurrence, with temperature figuring prominently in models with the majority of posterior support, and a model consisting of the single covariate, average monthly minimum temperature, showed by far the greatest posterior support. A comparison of alternative model averaging strategies was made with one strategy using the full posterior distribution and a simpler approach that utilized the majority of the posterior distribution for predictions but with vastly fewer models. Both BMA approaches showed excellent predictive performance with little difference in their predictive capacity. Applications of BMA are still rare in ecology, particularly in management settings. This study demonstrates the power of BMA as an important management tool that is capable of high predictive performance while fully accounting for both parameter and model uncertainty.

Key words: Bayesian model averaging; Deception Bay, Queensland, Australia; harmful algal bloom (HAB); Lyngbya majuscula; *Occam's window; predictive model; receiver operator characteristic (ROC) curve; reversible jump Markov chain Monte Carlo (RJMCMC).*

Introduction

Harmful algal blooms (HABs) are a worldwide problem. These blooms cause substantial damage to affected ecosystems, increasing turbidity and smothering aquatic plants, thereby damaging important invertebrate and fish habitat (Paerl and Huisman 2008). Some species are toxic, leading to significant human health concerns (Osborne et al. 2001). There has been a considerable escalation in both extent and duration of HABs, particularly in many estuaries and coastal waters over the past several decades (Anderson et al. 2002).

One species of concern is *Lyngbya majuscula*, a nuisance cyanophyte with a worldwide distribution. Problems with *Lyngbya* blooms including substantial adverse ecological, economic, and human health impacts have been noted in areas as diverse as Florida, Hawaii, Japan, and Australia (Arthur et al. 2006). In Australia, *Lyngbya* blooms can have severe ecological impacts by smothering and destroying seagrass beds (Dennison et al. 1999) that act as valuable breeding habitat for fish

and food resources for dugong (*Dugong dugon*). Impacts on fish populations cause substantial and ongoing effects on commercial and recreational fishing in the area. *Lyngbya* is toxic to humans, containing chemicals that cause asthma, dermatitis, and eye irritation (Osborne et al. 2001).

As with most HABs, managing *Lyngbya* blooms has proved to be problematic. It has been recognized that there are a variety of causative factors for HABs which may be species and even location dependent (Anderson et al. 2002). While this suggests that generic solutions for the management of HABs may be difficult to achieve, predicting the occurrence of blooms in specific areas would be of obvious benefit to enable the development and implementation of appropriate mitigation strategies. Consequently, several studies have used statistical models to make species and site specific HAB predictions for a variety of species (e.g., Lee et al. 2003, Chau 2005, Muttil and Chau 2006, Lui et al. 2007).

Despite the considerable advantages that predictive algal bloom models may confer for ecological management, it is important to recognize the need to acknowledge uncertainty in any modeling approaches. Models have a structure, including the parameters that are used in the model and estimates of the parameters that are

particular to that structure. If model predictions are incorrect, for instance because parameter estimates are wrong, this may prove costly in ecological management programs. There is an increasing consensus that uncertainty regarding parameter estimates of ecological models must be taken into account (Ellison 1996).

Together with parameter uncertainty, however, there is often also uncertainty regarding the selection of the models to best explain observed responses (Chatfield 1995, Draper 1995). Typically there are at least several, and often a large number of models from which to select. In ecological studies it is still routine to assume that a single best model choice exists, and to proceed as though this choice were known to be correct in making predictions (Draper 1995, Wintle et al. 2003). If the predictions from alternative plausible models are different, there are hazards in relying on a single model. This may lead to overconfident predictions, making management decisions based on these predictions more risky than might be supposed (Hoeting et al. 1999). Given that the scale of HAB impacts as well as management programs may be large scale, this creates a substantial onus on modelers and managers to ensure that all sources of uncertainty are adequately accounted for.

The Bayesian paradigm has been recognized as a useful framework for the effective management of ecological problems (Ellison 1996, Wade 2000, Dorazio and Johnson 2003), in part due to acknowledgement of parameter uncertainty in the posterior distribution. Bayesian analysis also allows practitioners to sift through a multitude of possible predictive factors and relationships to determine which models are the most plausible given the observed data (Ellison 2004). In a Bayesian setting, methods for discriminating among these possible solutions to find a "best" model have included Bayes factors (Kass and Raftery 1995), the Bayesian Information Criterion (Schwarz 1978) and the Deviance Information Criterion (Spiegelhalter et al. 2002).

Rather than ignoring model uncertainty in the search for a "best" model, a more satisfactory solution is to use Bayesian model averaging (BMA) techniques, where an average model is constructed by the combination of individual models weighted by their degree of plausibility (Raftery et al. 1997, Hoeting et al. 1999, Wintle et al. 2003). By averaging over many different competing models BMA incorporates model uncertainty into conclusions about parameters and prediction. While BMA can be achieved via a number of techniques, reversible jump Markov chain Monte Carlo (RJMCMC; Green 1995) is an efficient algorithm that allows for the simultaneous estimation of parameter values and model structure, together with estimates of plausibility that can be applied to individual models (Link and Barker 2006). This obviates the need for a separate model selection step. Although BMA is now a standard statistical technique, it is still rarely used in ecological studies (Ellison 2004, King et al. 2006), with use in management

virtually unknown (although see Thomson et al. [2007] for the use of BMA to predict bird species distributions).

There are a spectrum methods that have been employed for BMA depending on the intent of the modeling (ranging from explanation to prediction), and the size of the available data set. For example, Stow et al. (2004) used Bayes factors to weight and average over a small number of previously published mechanistic models in order to predict declines in fish tissue PCB concentrations, and to gain insight into the mechanism by which this might be occurring (see also Qian et al. [2004] for another example). Alternatively, "data mining" approaches (e.g., Smith and Kohn 1996) can be used for predictive modeling when large amounts of data are available and explanations of ecological process are of less interest. Often, however, modelers and managers are faced with an intermediate situation in which data are limited, and some knowledge of the ecological processes involved is available, but the extensive prior knowledge needed to construct plausible mechanistic models is lacking. We propose here a method by which the careful selection of ecologically relevant variables and the use of BMA leads to the capacity for robust predictions while giving some insight into mechanisms of the ecological process under consideration.

In the current study, we demonstrate the utility of BMA in predicting occurrences of HABs while fully accounting for both parameter and model uncertainty. As a specific example, we focus on *Lyngbya majuscula* blooms in Deception Bay, a small embayment near Brisbane, Australia. We consider both the predictive capacity of the approach and the ecological significance of the models identified. We also compare the predictive capacities of alternative model averaging strategies, using both the full posterior distribution and a simpler strategy in which many fewer models are used to predict bloom occurrences.

METHODS

Lyngbya bloom data.—*Lyngbya* occurrence data were accessed from the Queensland Environmental Protection Agency website (EPA 2007) for the period January 2000 to May 2007. These monthly observations were supplemented with data from a *Lyngbya* bloom in 2000 (Watkinson et al. 2005), providing a total of 77 observations.

Covariate data and selection.—Algal blooms are complex phenomena, and there has been considerable research into the causes of *Lyngbya* blooms in Deception Bay. These studies range from an investigation of the effects of iron on *Lyngbya* blooms using a process model (Arquitt and Johnstone 2003) to various observational (Albert et al. 2005, Watkinson et al. 2005, Arthur et al. 2006) and experimental (Watkinson et al. 2005, Ahern et al. 2006a, b, 2007) studies. As with many complex problems, the knowledge and data gained from

these studies had not previously been consolidated, making statistical analysis difficult.

One difficulty with predictive modeling can be the inclusion of candidate models that have high predictive value but little biological meaning, and are thus difficult to interpret. In order to select appropriate covariates for this study we made use of the results from a previous Bayesian net (BN) modeling study. In this study, the BN model structure was created using the expert opinion of a scientific reference group, and data, process models and expert opinion were synthesized to populate the model (Hamilton et al. 2007). This modeling highlighted the importance of environmental factors in driving the first stages of *Lyngbya* blooms (Hamilton et al. 2005). Both light and temperature were environmental variables were found to be influential on *Lyngbya* blooms in the BN analysis.

While water temperature was used as a variable in the BN analysis, water temperature data were not available at the temporal frequency and for the extent of the *Lyngbya* bloom data in the current study. Air temperature forms a good proxy for water temperature since there is typically only approximately a one degree difference between air and water temperatures. In their intensive study of a single *Lyngbya* bloom in Deception Bay, Watkinson et al. (2005) measured average daily temperature. Given that the observed data set in the current study was longer than the Watkinson et al. (2005) study, but with coarser temporal resolution, we rather considered average monthly minimum (min-Temp) and average monthly maximum temperatures (maxTemp).

We accounted for the BN variable Light using two covariates in the current model. To account for incipient radiation we took total daily solar exposure and calculated a monthly average (solex). We also included a covariate to account for the amount of sky that was not covered by cloud (clearSky). Using daily cloud cover measured in octets at 09:00, 12:00, and 15:00 hours, we calculated the amount of sky not covered by cloud at each time period, summed these across each day, and calculated a monthly average.

In the BN analysis, the amount of nutrients available in the water column was also found to be influential on the *Lyngbya* bloom node. Thus although the concentration of available nutrients would ideally be the next candidate according to the BN analysis, there are no appropriate data for dissolved nutrients in Deception Bay that cover the observational period modeled. Rainfall substantially influenced available nutrients in the BN analysis, however (Hamilton et al. 2007). There was also a strong belief in the scientific expert reference group that rainfall promotes the flow of nutrients into Deception Bay and thus is closely linked to bloom initiation. To test the hypothesis that rain influences *Lyngbya* occurrences, total monthly rainfall (rain) was also included as a candidate variable.

In addition to analyzing the series of *Lyngbya* bloom data with covariate data in the same temporal frame, we consider the possibility of a time lag in the influence of environmental covariates on *Lyngbya* bloom occurrence. There was a firm belief within the expert group that environmental factors in the period preceding a *Lyngbya* bloom strongly influence the probability of that bloom occurring. To examine this hypothesis we include as covariates one-month time lags on clearSky, rain, solex, minTemp, and maxTemp. While we are unaware of any ecological evidence to suggest a one month time lag is reasonable, we have used this as a pragmatic consideration due to the temporal scale of available data. Note that, while there were 77 data points for each environmental variable, introducing one-month lag terms in the model reduces the number of bloom observations available for modeling from 77 to 76. We also consider the possibility that covariates do not act in isolation to influence *Lyngbya* occurrences, but that interactions between covariates may have a major effect. We therefore also include a range of interaction terms. The saturated model included 17 terms, as 10 main effects and seven interactions (minTemp × lag1Rain, maxTemp × lag1Rain, lag1ClearSky × minTemp, lag1ClearSky × maxTemp, Solex × ClearSky, lag1Solex × minTemp, lag1Solex × maxTemp).

All covariate data were sourced from the Bureau of Meteorology. Monthly rainfall data were obtained for the area covered by one degree of latitude and one degree of longitude (152°30′ E to 153°30′ E and 26°30′ S to 27°30′ S). The area contained within these points covers the majority of the catchments that supply Deception Bay. Temperature, solar exposure and cloudiness data were obtained for Brisbane or Brisbane airport meteorological stations. These stations had records of sufficient length and are in close proximity to Deception Bay. Although most records were complete, 11 solar exposure observations were not available.

Note that, although the previous Bayesian net modeling provided invaluable insights into the appropriate ecological variables to select, the same data sets were not used in the current study.

Statistical model.—From a statistical modeling perspective, each covariate or combination of covariates which is assessed is viewed as a separate hypothesis or model. Using a Bayesian approach, the probability of each model is evaluated in light of the data. While there are over 130 000 possible combinations of the 17 terms that were used in this analysis, one advantage of the RJMCMC algorithm is to evaluate and rank a large number of models according to their posterior probability.

The statistical model we employed is a Probit model with AR(1) dependence. The Z_i is the indicator of presence of a *Lyngbya* bloom at time i:

$$Z_i = \begin{cases} 0 & Y_i < 0 \\ 1 & Y_i \geq 0. \end{cases} \quad (1)$$

In the model, a bloom occurs if the latent variable Y_i is zero or greater, otherwise an outbreak will not occur. This latent variable can be thought of as measure of the fitness of the environment for the spread of *Lyngbya*. The latent variable has two components. The first component ($\mathbf{x}$) is a deterministic contribution from the K measured explanatory variables (covariates) while the second component (e) is residual stochastic variation:

$$Y_i = \mathbf{x}_i \boldsymbol{\beta} + e_i \qquad (2)$$

where $\mathbf{x}_i$ is a K-component vector for the ith observation and $\boldsymbol{\beta}$ is a $(K + 1)$ vector of regression coefficients including an intercept term.

Given the nature of *Lyngbya* blooms (i.e., the possibility that blooms last for more than one reporting period, and therefore observations are not independent), possible time-series dependence is captured by modeling the random component as a stationary autoregressive AR(1) process:

$$e_i = \rho e_{i-1} + \xi \qquad (3)$$

$$\xi_i^{\text{iid}} \sim \mathcal{N}(0, 1 - \rho^2). \qquad (4)$$

The variance of the time series is constrained to be 1 for all values of ρ so that the scale of $\boldsymbol{\beta}$ is not affected by ρ. See Weir and Pettitt (2000) for a similar model in a spatial context. The prior for ρ was chosen to be uniform (-1, 1). The prior for $\boldsymbol{\beta}$ was chosen to be multivariate normal with mean zero and covariance matrix $\boldsymbol{\Lambda} = c \times I$ where I is the identity matrix. Selecting a value of c that approaches zero indicates very strong prior information that the coefficients should be close to zero. Conversely, as c approaches ∞, the prior is very uninformative. In our analysis, we selected $c = 10$, which seemed appropriate given the scaling of the covariates and the stochastic component e in Eq. 2 is restricted to have a variance of 1. The choice of c affects the possible size of regression coefficients, with larger values of c allowing for a greater possibility of larger regression coefficients. For example, selection values of c greater than 10 would indicate a prior belief that the occurrence of a HAB can be very accurately predicted based solely on covariate information. We did not believe this to be the case, particularly given that potentially important covariates (nutrient concentrations) were missing from the data set. The choice of $c = 10$ means that, a priori, each regression coefficient belongs to the interval (-6, 6) with approximately 94% probability. A uniform prior $U(0, 1, \ldots, 17)$ was placed on K, the number of variables included in a model. Given that K variables were included, each of the possible models were treated as equally probable a priori.

Since the solar exposure series involves missing observations, it was necessary to generate plausible values for the missing observations. To this end an ARIMA (0, 1, 0) model with Gaussian noise was adopted for this series. The variance of the noise was described a priori by a conjugate prior, an inverse gamma (1, 1). Sampling the variance parameter and the missing values from the posterior distribution is straightforward using Gibbs sampling.

The RJMCMC algorithm was developed using the R statistical package (R Development Core Team 2007), and is available from the authors upon request. The RJMCMC algorithm was run for 520 000 iterations with the first 20 000 iterations discarded as burn-in. In each iteration, the algorithm proposed a perturbation of the existing model (such as the inclusion or exclusion of a covariate) and accepted the model with some probability. The number of acceptances of any model divided by the total number of iterations forms the posterior probability of that model, and denotes the degree of belief that should be placed in the model given the current data. These can be used to form model weights for selected models (Link and Barker 2006).

It would be possible to extend this model to include basis functions and thus allow for the possibility of non-linear predictors. Prediction becomes very challenging when there are many variables and few data, however. In light of the limited HAB data available for this system, we have restricted ourselves to a ecologically relevant variables and a linear modeling space in order to avoid degrading the predictive performance of the model. Note, however, that if a standard probit regression with stepwise variable selection was performed, it would be expected to perform poorly due to an inability to account for the temporal dependence in the data.

Comparison of alternative model averaging strategies.—By accounting for model uncertainty BMA minimizes prediction risk, and has also been shown to improve model prediction accuracy on average (Hoeting et al. 1999, Wintle et al. 2003, Link and Barker 2006). A practical consideration in the use of a BMA strategy is the potentially large number of competing models in the posterior distribution (also known as the combined or averaged model), since for n covariates evaluated by the RJMCMC algorithm there will be 2^n models in the averaged model. Since in the averaged model individual models are weighted by their degree of plausibility, it has been proposed that models that predict the data "far less well" than the best model could be excluded in a strategy known as Occam's window (Madigan and Raftery 1994). We evaluated two alternative strategies: averaging over all sets of predictors in the posterior ("full BMA") and an Occam's window approach, in which we averaged over those models that constituted an arbitrary threshold of 75% of the posterior support.

Posterior predictive checks.—We employed posterior predictive and calibration checks to ascertain the utility of each of these approaches as predictors of *Lyngbya* occurrences under the current data set. Cross validation is a method which allows for the estimation of approximately unbiased prediction error/misclassification rates. The procedure involves splitting the original

TABLE 1. Models accounting for approximately 75% of the posterior support from 500 000 MCMC iterations (α intercept) to predict occurrence of *Lyngbya majuscula* algal blooms in Deception Bay, Queensland, Australia.

Model number	Model description	Posterior support (%)
1	minTemp + α	48
2	maxTemp + α	7
3	α	6
4	minTemp × lag1Rain + α	5
5	lag1Rain + minTemp × lag1Rain + α	4
6	lag1Solex × minTemp + α	2
7	minTemp × lag1Rain + maxTemp × lag1Rain + α	2
8	lag1minTemp + α	1

Notes: Solex is the monthly average of daily measurements of total daily solar exposure. Air temperature forms a good proxy for water temperature since there is typically only approximately a 1°C difference between air and water temperatures.

data set into training and test sets. The model is then fitted to the training set and predictions of the data in the test set are formed using this model. The predictions are compared to the test set and a summary of the accuracy is made.

Here we followed a "leave one out" procedure, where observations were sequentially excluded from the original data set and predicted using the remaining training set. Results of each of the cross-validation procedures were summarized in a receiver operator characteristic (ROC) curve. ROC curves assess the predictive power of a model (Fielding and Bell 1997). In brief, the ROC curve is formed by plotting the empirical probability of incorrectly predicting occurrence (1 − specificity) against the empirical probability of correctly predicting observed occurrences (sensitivity) for all possible threshold levels. ROC curves are typically summarized using the AUC (area under the curve) statistic. An AUC statistic of 0.5 would be expected by random guessing (i.e., from a classifier with no discriminating power) and an AUC of 1 indicates a perfect classifier. Values of 0.7–0.9 indicate a useful range, with values of above 0.9 indicating high accuracy (Swets 1988). For a more detailed explanation of ROC curves and the AUC statistic in an ecological context see Manel et al. (2001).

A calibration curve aims to assess the accuracy of probability statements. A prediction method is said to be well calibrated if those events which are predicted to occur with probability *p* actually occur *p* × 100% of the time (see Dawid [1982] for a discussion of calibration in a Bayesian setting). Nonetheless, a method can be well calibrated but give poor predictive accuracy. If the long run relative frequency of HAB occurrence was calculated the prediction would be well calibrated. However, such predictions would not be very useful. The calibration curve in this instance would be a single point on the diagonal line. On the other hand, the ROC curve summarizes the accuracy of the prediction. From each point on the ROC curve we can calculate the misclassification rates for a given choice of threshold. A model with good predictive accuracy as indicated by a high

AUC can be poorly calibrated since the ROC curve will not change under monotone transformations of the prediction variable while the calibration curve will. In the current study, the prediction of occurrence probabilities from the cross validation procedure in the calibration curve were compared to the actual *Lyngbya* occurrence data using a loess smooth (Cleveland and Devlin 1988).

Forecasting HABs.—To construct the predictive model in the current study, we have assumed that the future covariates were known. To assess the capacity for this method to forecast *Lyngbya* blooms in Deception Bay, we used all covariate data up to a chosen period, and predicted the probability of a *Lyngbya* bloom for the following month. We did this for six consecutive months, commencing from time period 64. That is, we used all covariate information up until time period 63 to predict the probability of a bloom for time period 64, all covariate information up until time period 64 to predict the probability of a bloom for time period 65, and so on. We compared these prediction probabilities against known occurrence or absence of a bloom during this time period.

RESULTS

890 models were evaluated using the RJMCMC algorithm. We averaged over this full model set to assess predictive accuracy in the full BMA strategy. Of the 890 models, 882 occurred with a low posterior probability and contributed to the lower 25% tail of the total posterior mass. These models may contribute little to the explanatory power of the analysis while adding considerably to its complexity, and were excluded under the Occam's window strategy. Eight models formed the top 75% of the posterior probability mass (Table 1). All models in this set included an intercept term α.

Model 1, comprising the single term average monthly minimum temperature, presented by far the best single model, accounting for almost half the posterior support of all models, and approximately seven times the posterior support of the next best model (Table 1). The posterior probability of occurrence of *Lyngbya* as a
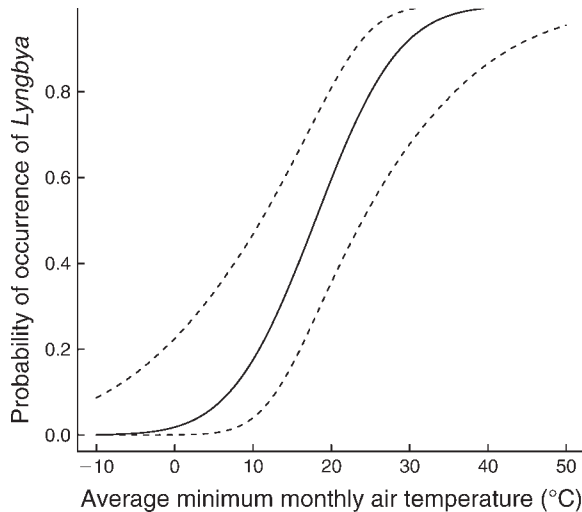
FIG. 1. Predicted occurrence of algal blooms of *Lyngbya majuscula*, a toxic cyanophyte, in relation to air temperature in Deception Bay, Queensland, Australia. Shown is the probit curve for the model with the highest posterior support (model 1) with 2.5% and 97.5% credible intervals (dashed lines). This was constructed by sorting all cases of the highest posterior probability model and selecting the median probit curve, with 95% credible intervals represented by 2.5 and 97.5 quantile curves. Air temperature forms a good proxy for water temperature since the difference is typically ~1°C.

function of this model is plotted in Fig. 1. The second-best model had only 7% posterior support (Table 1) and again consisted of a single temperature variable (average monthly maximum temperature). In fact, temperature was a component in seven of the eight models in this subset.

Posterior predictive checks.—ROC curves for the two modeling strategies are shown in Fig. 2. Both BMA strategies showed excellent classification capacity, with essentially no difference between full BMA (AUC = 0.92) and the Occam's window strategy (AUC = 0.91). Model calibration for the two strategies are shown in Fig. 3. For a well-calibrated prediction method, the smoothed curve should be the line connecting the points (0, 0) and (1, 1). From these plots, it is apparent that each of these strategies are well calibrated and so the predicted probabilities of occurrence have a meaningful interpretation.

Forecasting HABs.—The results of forecasting *Lyngbya* blooms one month into the future, and comparison with known blooms at this time period, are presented in Table 2. Generally, it can be seen that a high predicted probability of a bloom coincided with an actual bloom having occurred, and a low predicted probability of a bloom coincided with no bloom occurring.

DISCUSSION

In this study, we demonstrate BMA as a highly useful approach to predicting HABs in coastal waters while accounting for uncertainties in model structure (Table 1)

and parameter estimates (Fig. 1). Additionally, we demonstrate that unlike automated model selection techniques that may select parameters with no real relationship to the dependent variable (Derksen and Keselman 1992), careful selection of covariates allows the models identified by BMA to be meaningfully interpreted in an ecological context.

While accounting for model uncertainty with BMA has been demonstrated to provide more accurate predictions than using model selection (Raftery and Zheng 2003, Thomson et al. 2007), and will thus be a superior approach in a typical management situation where the costs of incorrect predictions may be high, the complexities introduced by considering a large number of models in the posterior may be considerable. We demonstrate that in this study there was essentially no difference in predictive accuracy between the two BMA strategies. The 882 models comprising the lower 25% of
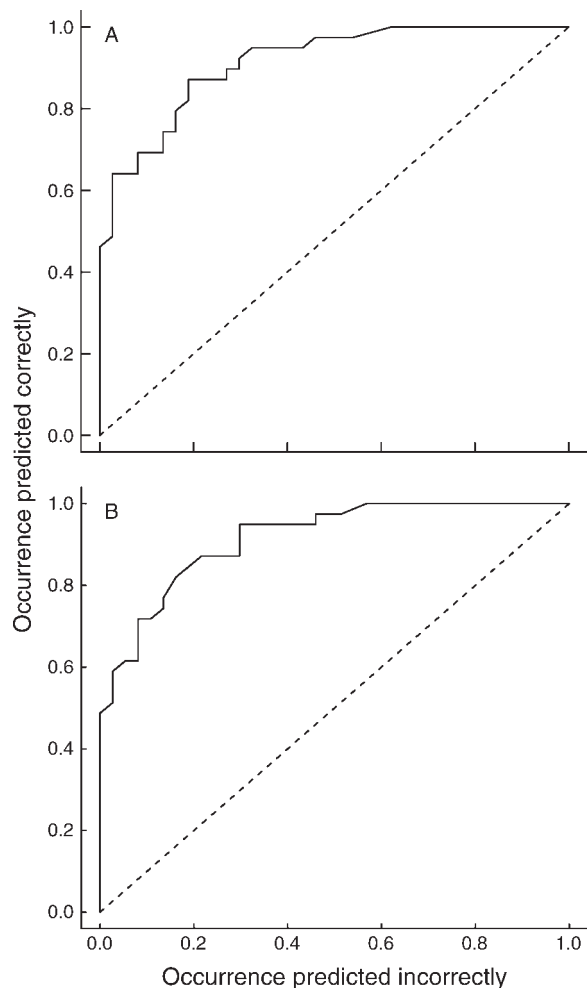

FIG. 2. Receiver operating characteristic (ROC) curve for *Lyngbya* occurrence predictions using (A) the full posterior distribution (full Bayesian model averaging, BMA) and (B) the Occam's window strategy. The dashed line represents an ROC curve that could be expected using random guessing.
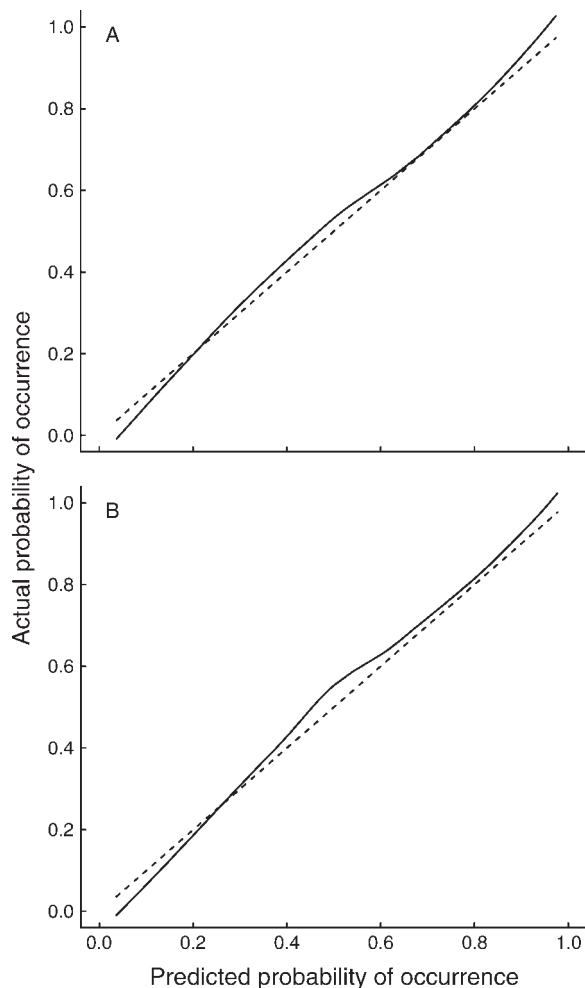
FIG. 3.   Calibration check for the predictive models using a loess smooth for *Lyngbya* occurrence predictions: (A) the full posterior distribution (full BMA) and (B) the Occam's window strategy. The dashed lines represent a perfectly calibrated model.

the posterior clearly added little predictive power, and in this study utilizing these models would present a considerable increase in complexity with no appreciable gain.

An accurate predictive modeling strategy such as BMA can form a sound basis for the management of complex environmental problems in the face of multiple sources of uncertainty. If the objective of a manager is to simultaneously minimize the risk of incorrect predictions, maximize predictive accuracy and minimize the complexity of results, in this study it would appear to be most advantageous to proceed with an Occam's window strategy. However, when the posterior probability of one model far exceeds that of any other managers may prefer to trade off the accuracy of BMA against the simplicity of model selection. It has been argued that a model selection approach may be justified given sufficient plausibility for a single model (Burnham and

Anderson 2002); however, this will be unknown until model uncertainties have been estimated. We suggest that such choices will depend on the particular problem at hand, depending among other things on the plausibility of the single model, any advantages gained by using a simpler predictive approach and an assessment of the risk and consequences of incorrect predictions. In employing such an approach managers should aim for a good trade-off between accurate prediction, model parsimony and pragmatism. In the current study, the strength of posterior support for average minimum monthly temperature could be used to provide a rough "rule of thumb" indicator for assessing the probability of *Lyngbya* blooms. Using model 1 together with predictions of minimum temperature would provide a simple predictive tool. The Occam's window approach we employed in the current study was to run the RJMCMC algorithm, identify the full posterior model, and then predict *Lyngbya* bloom occurrences based on the top 75% of the posterior mass. While there was little loss of predictive power in the current study, the advantage to this approach in the current study was that it vastly improved the interpretability of the averaged models. It should be noted, however, that the predictive power of individual models will decrease as the posterior support for that model decreases.

As we have demonstrated, it is possible to forecast *Lyngbya* blooms in Deception Bay and attain reasonable prediction probabilities that coincided well with actual bloom observations (Table 2). For the practical application of this method to forecasting *Lyngbya* blooms in Deception Bay, a number of aspects would need to be considered however, including the amount of posterior support used to make predictions (which will affect the covariate data required) and the accuracy of available covariate forecasts. For example, if managers chose to use the full Bayesian model averaging approach, the same set of covariates as used in the current study would need to be predicted for future periods. If the simpler Bayesian model averaging approach which averaged over those models providing 75% of the posterior support were to be applied, then the Clear Sky variable would not need to be used. Taking

TABLE 2.   Comparison of predicted probabilities of a harmful algal bloom (HAB) and actual occurrence of a *Lyngbya* bloom in Deception Bay, Queensland, Australia (1, bloom occurred; 0, bloom did not occur) for six consecutive time periods.

Time period	Predicted probability of bloom occurrence	Actual bloom occurrence
1	0.19	0
2	0.12	0
3	0.07	0
4	0.65	1
5	0.84	1
6	0.9	1

this further, considering only 60% of the posterior only need maximum and minimum monthly temperatures would be required. Note, though, that when considering an Occam's window approach, it would be necessary to recognize that HAB predictions may not be as accurate as those made using the full posterior model, depending on how much of the posterior mass is retained for prediction.

The approach we have outlined here could also be employed for the prediction of HABs in other regions. One practical consideration may be that ecological differences in HAB dynamics might exist in other areas, and so careful consideration would need to be given to the candidate variables that were selected.

Although prediction of *Lyngbya* blooms was the principle focus of this study, interpretation of the ecological factors driving blooms will also be important for ecological management. One potential problem with BMA, or indeed any predictive strategy, is the inclusion of candidate models that may have high predictive value but make little sense ecologically. The selection of candidate variables is a particularly challenging aspect of modeling with little guidance available. In the current study, we have carefully selected covariates that allow for meaningful ecological interpretation of results.

The results for the Occam's window strategy show that there are a suite of useful predictive factors for *Lyngbya* blooms in Deception Bay, including average minimum and maximum monthly temperature, rain in the month previous to a *Lyngbya* bloom, solar irradiance and a number of interactions among these variables. The most striking result, however, is the influence of temperature on *Lyngbya* blooms, with temperature covariates in seven of the eight most plausible models. The strong influence of average minimum monthly temperature on *Lyngbya* occurrences is particularly notable, with the strong posterior support for this model approximately seven times the weighting of the next most influential model (average maximum monthly temperature).

The recognition that temperature plays a strong role in *Lyngbya* bloom occurrences confirms the work of Watkinson et al. (2005), who found that average water temperatures in excess of 24°C were important for the initiation of a *Lyngbya* bloom in Deception Bay. Other studies have either noted the importance of water temperature in promoting algal blooms (Watkinson et al. 2005, Edwards et al. 2006, Lekve et al. 2006), or utilized water temperature to model algal blooms (Chen and Mynett 2004, Oh et al. 2007). Interestingly, however, we found no other studies to date that have focused on minimum temperatures as an important predictor of coastal algal blooms. This is an important recognition, since it will enable more discriminating predictions of *Lyngbya* blooms in Deception Bay based on meteorological forecasts, and may better inform other studies.

The usefulness of predictive models can be judged by their accuracy (Swets 1988). Errors in prediction can be attributed to "algorithmic" errors, largely imposed by limitations in the classification method, and "biotic" errors, when not all aspects of an organism's biology have been adequately modeled (Fielding and Bell 1997). While the predictive accuracy of the BMA strategies employed here is demonstrated by high AUC statistics, one surprising aspect of this result is the accuracy of predictions in the absence of dissolved nutrient data. A number of studies have highlighted the importance of nutrification in promoting algal blooms, including recent laboratory and field studies specifically examining the effects of nutrients on the growth and blooms of *Lyngbya* majuscula (Elmetri and Bell 2004, Ahern et al. 2006a, b, 2007). Several of these studies suggest the longer term importance of reduction in nutrient loads to Deception Bay. Consequently the capacity for the model to predict blooms well without the inclusion of long term dissolved nutrient data is worthy of closer scrutiny.

One explanation for this apparent conflict may be that a proxy variable adequately accounted for dissolved nutrients in the model. While rain is believed to influence dissolved nutrients in Deception Bay, and thus was included in the modeling, it had relatively poor predictive ability. Total monthly rainfall in the month of a *Lyngbya* bloom had very little posterior support and was not present in the models comprising the top 75% of the posterior. Rain in the month previous to a *Lyngbya* bloom occurred with a low weighting either as an independent term (model 5) or as part of an interaction term (models 4, 5, and 7). Together, these models account for only approximately 11% of the total plausibility of all models in this model set. This may be due to nutrient levels within the bay being above some critical threshold during the time period modeled therefore allowing blooms to be triggered by solely environmental factors.

Alternatively, it may be that temporal variations in dissolved nutrient concentrations do in fact play a significant role in bloom formation, but have not been accounted for in the covariates evaluated by the RJMCMC algorithm. This may account for the occurrence with some plausibility of model 3 in the posterior distribution, consisting solely of an intercept term (Table 1). Much of the predictive power here is due to the correlation in the error structure of the model. This allows the intercept-only model to be quite competitive and its simplified model structure leads to significant posterior support. A likely explanation for this is that one or more important covariates possessing significant temporal correlation (such as dissolved nutrient concentrations) have not been measured. Hence, in this model the error term attempts to take advantage of the correlation in order to act as a surrogate for the true predictor. Finally, the modeling may be limited both by the relatively short length of the time series and by the extent of the covariates.

Observations under more diverse environmental conditions may assist in understanding the important factors of *Lyngbya* blooms.

The severe ecological damage and possible human health consequences due to HABs demonstrate a pressing need to implement the best possible modeling and management strategies for this problem. Unfortunately, this is a common problem in many areas of ecological management. Although the advantages Bayesian modeling are being increasingly recognized in ecology (Ellison 2004), BMA has not seen widespread use in the management of ecological problems. The unwillingness to fully recognize structural uncertainties in applied ecology may be because software for implementing algorithms such as RJMCMC has only recently become available, or may relate to a reluctance to move beyond a "best model" paradigm. The use of automated model selection procedures in software such as stepAIC or the DIC function in WINBUGS might also inadvertently accentuate this pattern (Ellison 2004). As we have shown here, BMA provides a powerful and effective framework for the identification of ecologically interpretable models, and accurate prediction of complex ecological problems.

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