Management-oriented modelling of blue-green algal blooms: an example from Bourke Weir, NSW, Australia

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17 Abstract
18
19 We describe an algal population model that deliberately moves away from the current trends in algal
20 population modelling of increasing complexity and increasing data requirements. The process-based
21 model is conceptually simple, and functional relationships and process parameter values within the
22 model are drawn from existing research. Our model is driven by standard monitoring data. This
23 contrasts with most published models, which rely on the collection of extensive data sets, and which
24 require a great deal of information about the water body being modelled. Because the collection of
25 these data is costly and time consuming, there is a real need for models that can be driven by
26 standard monitoring data. The benefit of such an approach for management is the potential portability
27 of the basic model between different sites. The model was initially developed for the population of the
28 main bloom forming cyanobacterium, *Anabaena* sp., in Bourke Weir, New South Wales (Australia),
29 part of the Murray-Darling Basin. The model simulated each of the population peaks that occurred
30 over a 10-year period 1992 – 2002, but also incorrectly predicted another peak. A sensitivity analysis
31 showed that the model's ability to predict the bloom status of the system was generally robust to
32 moderate (±10%) perturbations in process parameters and driving data values. However, perturbation
33 of temperature had noticeable effects on the height of population peaks. Despite being based on
34 simplified relationships, the model simulated the onset of cyanobacterial blooms with sufficient
35 accuracy to warrant further development of the approach as a management tool. Minimising the data
36 requirements increases the likely portability of the model to other sites. Moreover, keeping the model
37 deliberately simple increases the likelihood of being able to use it in a predictive sense for future
38 management of cyanobacterial blooms.
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40 KEY WORDS: water quality management; process-based model; bloom; cyanobacteria; blue-green
41 algae; *Anabaena*
42

1. Introduction

In recent years, reports of cyanobacterial blooms have increased in many countries (Whitton and Potts, 2000). These blooms represent an enormous challenge for water quality management the world over, because of effects such as stock deaths due to contaminated water (e.g. Beasley, et al., 1989), liver failure (e.g. Jochimsen, et al., 1998) and increased cancer rates (e.g. Yu, 1994) in human populations, and loss of tourism-based revenue (e.g. Walker and Greer, 1992). Early research indicated the importance of phosphorus availability in determining average algal biomass in lake systems (e.g. Dillon and Rigler, 1974), and as a consequence, anthropogenic eutrophication (increased nutrients that derive from human influences) is often seen as the root cause of excessive algal growth (e.g. Smith, et al., 1999). However, other factors have also been shown to be important in mediating bloom formation. These include a stable water column, warm weather, high incident irradiance, enhanced organic matter loading, and selective activity of grazers (Paerl, 1988). Minimisation of the severity and frequency of cyanobacterial blooms is a key target for many 'whole-of-catchment' management strategies (e.g. GBCMA, 2003). Effective management of cyanobacterial blooms requires an understanding of the local conditions that favour bloom formation. However, since many factors determine whether or not a bloom will form, methods are required that are able to integrate the effects of various environmental variables. Modelling is one technique that can provide such integration.

A number of models already exist that seek to simulate cyanobacterial populations (e.g. Whitehead and Hornberger, 1984, Lung and Paerl, 1988, French and Recknagel, 1994, Howard, et al., 1995, Easthope and Howard, 1999, Everbecq, et al., 2001, Maier, et al., 2001, Reynolds, et al., 2001). Many of these models utilise environmental data for a large range of parameters (e.g. Yabunaka, et al., 1997) and/or at a fairly fine spatial / temporal scale (e.g. Lewis, et al., 2002). The existence of such data sets is the exception rather than the norm. Monitoring data will commonly only be available for a small selection of parameters, and at an irregular time scale that tends to be reactive to bloom status (Kneale and Howland, 1997). A model that is likely to find broad use in cyanobacterial management must be able to be driven by such data.

Models of various aspects of cyanobacterial biology or population dynamics are also tending towards greater and greater complexity (e.g. Laws and Chalup, 1990, Belov and Giles, 1997). The volume of work done to elucidate cyanobacterial biology and the characteristics of the physical environment they inhabit has facilitated this. Such models lead to detailed explanations of observed system behaviour, but will often not be of as much use for predicting future states as simple models (Scheffer and Beets, 1994). Simple models usually require less in the way of driving data and parameterisation, and so future scenarios can be modelled with greater confidence (Scheffer and Beets, 1994, Steel, 1997). Complex models are also far more computationally expensive, and recent work has demonstrated that for at least some aspects of cyanobacterial biology, they do not produce outputs that are noticeably different to those produced by simple models (Flynn, 2003). One must also consider the aim of the model. The needs of so-called policy models, such as the model described in this paper, are generally less stringent than for models designed for research (McIntosh, 2003). From a water quality management perspective, being able to predict the onset of cyanobacterial blooms is of prime importance. Currently in Australia, management decisions concerning reactions to algal blooms are based on the exceedence of 'alert levels' or thresholds based on cell counts or biovolumes (BGATF, 1992). Modelling threshold exceedence is a simpler exercise to creating an accurate and detailed model of all aspects of a cyanobacterial population, and the level of realism and accuracy required is less demanding.

Our aim, therefore, was to deliberately move away from the increasing complexity of algal population models, and to create a relatively simple model that could be run by standard monitoring data, and that could simulate the onset of cyanobacterial blooms (i.e. exceedence of a threshold value) with sufficient accuracy as to be potentially useful for informing management decisions. The model makes a number of assumptions and simplifications that are not entirely accurate, but which simplify the modelling process significantly. The likely effect of such assumptions is addressed in the discussion. The model is process-based so that it may potentially be applied to multiple sites without the need for site-specific calibration by extensive historical monitoring data. Moreover, we attempted to keep data

requirements as low as possible to increase the chances of model portability to sites with limited data, and of the model being useable in a predictive sense.

2. Methods

2.1 Background

The model has been initially developed for the population of the bloom-forming cyanobacterium *Anabaena* sp. in Bourke Weir, NSW, Australia. The model output was assessed against an exceedence threshold of 2000 cells mL^{-1}. The New South Wales Department of Infrastructure, Planning and Natural Resources (DIPNR) considers untreated drinking water unsafe for human consumption when cell concentrations of potentially toxic species such as *Anabaena* exceed this figure (BGATF, 1992). The choice of model species and site were dictated largely by readily available data, but both have relevance for other bloom prone systems throughout much of Australia and the World.

Anabaena circinalis is the most common bloom forming cyanobacterium in Australian inland waters (Jones and Orr, 2000), and members of the genus are common throughout the world. The cells form filaments that can control their buoyancy (Oliver and Ganf, 2000), and can thus float into well-lit surface waters during periods of reduced water circulation. *Anabaena* species also have the ability to fix atmospheric nitrogen (Oliver and Ganf, 2000). Bourke Weir is situated in northern New South Wales, Australia, and lies on the Darling River (Figure 1). Water is contained within the river channel, and so the weir is long and narrow. Similar weirs exist along the length of the Darling River. The waters in Bourke Weir are characterised by a high phosphorus content and turbidity is also generally high (Median values 1992-97: 0.13 mgL-1 TP, 80 NTU Mitrovic and Gordon, 1998). Over the last 15 years, Bourke Weir has been regularly subjected to cyanobacterial blooms. During the 1991 bloom that led to the establishment of the current algal-monitoring program, cell densities of *Anabaena circinalis* as high as 294,000 mL^{-1} were recorded in the weir (Bowling, et al., 1991).

2.2 Conceptual model

The numeric model is based on the conceptual model pictured in Figure 2. In the model, either light or phosphorus limitation, together with the effect of water temperature, regulate the daily rate of algal reproduction. Mortality reduces population numbers, as does a component representing the net number of cells washed from the weir each day. Flow determines the existence or otherwise of stratification in the weir, which governs mixing depth. Mixing depth combines with turbidity and day length to determine the extent of light limitation on population growth. Turbidity is also used as a surrogate for suspended solid concentration, which together with the algal population, determines the amount of bioavailable phosphorus for cell production.

2.3 Implementation

The model was implemented in Mathcad Professional 2001 (MathSoft Inc., 2000). It was driven by a Microsoft Excel 2000 (Microsoft ®, 1999) spreadsheet of monitoring data (see below), and delivered results to a separate sheet. The algal population was projected via a difference equation that calculated the number of cells mL^{-1} within the upper mixing layer (see below) of the weir each day.

2.4 Driving data

The model was driven by monitoring data for total phosphorus (P_{tot}), turbidity (Tu), temperature (Te), and flow out of the weir (F) measured at Bourke (Station 425003; Figure 1). Data were available for the period 7 September 1992 to 13 June 2002. Within this period, flow data were available daily. Data for P_{tot}, Tu and Te had been collected as single sub-surface (~20 cm depth; S. Dwyer, DIPNR, pers. comm.) samples from the Bourke gauging station, which lies approximately 6 km upstream of the weir wall, and were available at varying time intervals from daily up to approximately monthly. We used linear interpolation to provide a 'daily' data set. Day length (N) was approximated using a sine function that added (or subtracted) a proportion of a day length range to an average day length, depending on the date.

2.5 Model Functions

The functions, and the rationale behind each of them, are outlined below. The majority of calculations were performed for each day, but for ease of reading, most equations are presented without the $_t$ subscript. Parameter values and the sources of these data are outlined in Table I.

Flow related processes

Flow affected the population directly, via wash in / out, and indirectly via the mediation of water column stratification, which in turn affected light limitation (Figure 2). Both of these processes are affected by the mixing depth (Z_{mix}) - the thickness of the layer in which algae circulate. This parameter takes one of two values. If flow out of the weir is over a critical threshold (F_c), cells are assumed to circulate over the entire depth of the weir (Z_w). If flows are below this threshold, cells are assumed to circulate within an epilimnion of defined thickness (Z_e). Algae are washed from the weir at the ambient cell concentration (cA), and wash into the weir at a small nominal concentration (cA_{wi}). The model calculates the proportion of the mixing layer (V_{ex}) that enters and leaves the weir each day.

$$V_{ex} = F \div \begin{cases} Z_e \cdot W_w \cdot L_w & \text{if } Z_{mix} = Z_e \\ V_w & \text{otherwise} \end{cases} \quad (1)$$

The volume of the mixing layer is expressed as either the product of the weir's length (L_w), width (W_w) and the depth of the epilimnion for stratified flow, or as the entire volume (V_w) for non-stratified flow. The calculated mixing layer proportions are multiplied by the difference between cA and cA_{wi} and in the final population projection (Eq. 9) to determine the net number of cells per unit volume washed out of the weir on any given day.

Light limitation

Limitation of growth by light is mediated by mixing depth (Z_{mix}), water turbidity (Tu) and day length (N). We assume that growth is not limited by light until light falls below a saturating intensity (I_{sat}). Below this figure, growth decreases linearly with light to zero. This simple relationship has previously been applied to the modelling of growth-irradiance relationships (Bannister, 1979), and has also been successfully applied to photosynthesis-irradiance modelling (Jassby and Platt, 1976). In the model, surface irradiance is assumed to be constant throughout daylight hours, ignoring changes across the course of each day and with season. The coefficient of light attenuation (k) is expressed as an empirically determined linear function of turbidity (Oliver, et al., 1999).

$$k = 0.04 \cdot Tu + 0.73 \tag{2}$$

The depth at which I_{sat} is reached (Z_{sat}) is calculated using a transposition of the Beer-Lambert equation,

$$Z_{sat} = \frac{\ln(I_{sat})}{-k} \tag{3}$$

where I_{sat} is expressed as a proportion of the surface irradiance. We assume that algal cells are evenly distributed throughout the mixing layer. Depending on Z_{mix} and Tu, cells are subjected to one of two growth limitation regimens. First, if the cells circulate entirely within the well-lit zone ($Z_{mix} \leq Z_{sat}$), then growth is not limited. If Z_{mix} lies deeper than Z_{sat}, then growth is reduced for part of the time.

$$I_{lim} = \frac{N}{N_{\max}} \cdot \begin{cases} 1 & \text{if } Z_{mix} \leq Z_{sat} \\ \left(Z_{sat} + \dfrac{I_{sat} - \mathrm{e}^{-k \cdot Z_{mix}}}{k \cdot I_{sat}} \right) \cdot \dfrac{1}{Z_{mix}} & \text{otherwise} \end{cases} \tag{4}$$

Limitation between the depths $Z_{sat} - Z_{mix}$ is derived from the definite integral of the Beer-Lambert equation within this interval, and calculates the proportion of possible growth occurring over the depth

interval. The average limitation of light over the course of each day is scaled for day length so that light can only be truly non-limiting (I_{lim} = 1) on the longest day of the year.

Phosphorus availability and uptake rate

The driving data report total phosphorus (P_{tot}). This figure is converted into dissolved reactive phosphorus (P_{drp}), as it is a better estimate of the phosphorus pool available for algal growth. First, suspended particulate matter (*SPM*) is estimated using an empirical relationship between *SPM* and turbidity determined during the study of Bourke Weir by Oliver *et al.* (1999).

$$SPM = \max\left(\frac{Tu - 52}{0.67} \cdot 10^{-3}, 0\right) \quad (5)$$

To calculate P_{drp} available to produce cells at time *t+1*, the amount of phosphorus bound within cyanobacterial cells, and the amount bound tightly to suspended sediments are subtracted from P_{tot} at time *t*. Phosphorus bound within cells is expressed as the phosphorus quota of each cell (P_{cell}) multiplied by the projected population (*cA*). Phosphorus bound tightly to sediments is expressed as the concentration of suspended particulate matter multiplied by the average amount of phosphorus tightly bound to sediments (P_{spm}).

$$P_{drp} = \max\left(P_{tot} - P_{cell} \cdot cA - P_{spm} \cdot SPM, 0\right) \quad (6)$$

The proportional extent of phosphorus uptake limitation is then described by Michaelis-Menten kinetics.

$$P_{lim} = \frac{P_{drp}}{K_S + P_{drp}} \quad (7)$$

The maximum rate of phosphorus uptake (V_{max}) does not appear in the equation as the model only needs to determine the proportional extent to which the rate of P uptake is limited in order to calculate phosphorus limitation.

Temperature effects

In the model the rate of reproduction increases with temperature via a scalar, S_{Te}. The exponential relationship is modelled by

$$S_{Te} = \left(\sqrt[10]{Q_{10}}\right)^{Te-20} \quad (8)$$

In this case, the tenth root of the Q_{10} (the proportional increase in rate after a 10°C rise) gives the proportional increase for each degree C. The value of S_{Te} is 1 at 20°C, which is the temperature at which the basic rate of reproduction (r_{20}) was measured (see below).

Population projection

The population is projected using a difference equation that follows the basic structure: new pop = starting pop – mortality – net cells washed from weir + cells produced. The rate of reproduction is reduced by either light or phosphorus limitation (whichever is more limiting), and scaled according to temperature.

$$cA_{t+1} = cA_t - q \cdot cA_t - V_{ex_t} \cdot \left(cA_t - \cdot cA_{wi}\right) + \min\left(r_{20} \cdot \min\ (I_{lim_t}, P_{lim_t}) \cdot S_{Te_t} \cdot cA_t,\ \frac{P_{drp_t}}{P_{cell}}\right) \quad (9)$$

The basic rate of reproduction (r_{20}) was taken from the study of McCausland *et al.* (2002). The number of cells produced is the product of the modified rate of reproduction and the population. Occasionally, this calculation results in more cells being produced than can be supported by the amount of available

phosphorus. In these cases, the number of cells produced is constrained to the number supported by P_{drp}.

2.6 Sensitivity Analysis

We conducted a sensitivity analysis on the model in order to determine which parameters had the greatest effect on model output. We increased and decreased each of the model parameters and driving data streams in turn by 10%. Sensitivity was assessed by calculating the change in the percentage of days that exceeded the management threshold of 2000 mL^{-1}, and by inspecting plots of model behaviour. A second variant on the sensitivity analysis was also run, in which each of the three limiting scalars, I_{lim}, P_{lim}, and S_{Te} were set to 1 in turn.

3. Results

3.1 Model Performance

The population projected over the 10-year period was compared to monitoring data for *Anabaena* sp. cell numbers in Bourke Weir for the same period. The monitored data and modelled population are presented in Figure 3. The model only had limited success in forecasting actual cell concentrations. However, this is not a requirement for a policy model designed to emulate threshold exceedence. Figure 3 shows that the model predicted some elevation of cell concentrations in 8 of the 10 years, but that only six of these peaks reached 2000 cells mL^{-1}. The model managed to forecast each of the four major peaks in cell concentration (late 1992, late 1994, late 1995 and late 2001), and one minor peak in cell concentration (early 1999) that occurred during the validation period. However, the first and last forecast peaks persisted for much longer than did the actual blooms. The model also falsely predicted one peak that did not occur (late 1997). For the modelled population, blooms occurred during periods of low flow and low turbidity, which led to low light limitation in the system; and of high temperature, which increased the growth rate. Phosphorus did not limit population growth rate, but the total pool of phosphorus available limited the size of blooms. In general, blooms were dissipated by a sudden increase in flow.

3.2 Sensitivity Analyses

Table II shows the numeric results of the sensitivity analysis. The great majority of perturbations had little effect on model performance. Plots of the five most sensitive parameters (*Te*, r_{20}, q, Q_{10}, F_c) are shown in Figure 4. For the most sensitive parameter, *Te*, the plot shows that a ±10% change can change the status of 5 of the 8 population peaks from ‘bloom’ to ‘non-bloom’ and vice versa. The severity of the effect drops rapidly with less-sensitive terms. For r_{20}, the range of possible peak heights is reduced, and 4 of the 8 peaks can have their bloom status altered by perturbation. Perturbation of mortality, q, has a relatively consistent effect across all peaks, as should be expected of a constant loss rate. For Q_{10}, the effects are quite minor for all but the second and sixth peak. Both of these

peaks occur late in summer, when water temperatures are at their maximum. Hence it is not surprising that perturbing Q_{10} has an obvious effect at this time. The only other plot that showed any real visible effect was that for F_c, and this was restricted to the sixth peak. An examination of the driving data revealed that a large number of flow readings at this time were near the value for F_c. Thus the localised effect of the perturbation could be expected.

The effects of setting the limiting scalars to 1 are displayed in Figure 5. The results show that I_{lim} is the most important scalar for model function. In contrast, setting P_{lim} to 1 has almost no effect on model output. It should be noted, however, that in setting P_{lim} to 1, the total number of cells that can be produced any day is still limited by the total amount of available phosphorus (Eq. 9); only the rate of cell production is not limited by P-uptake considerations. Setting S_{Te} to 1 effectively models the population at a constant 20°C. Thus the timing and magnitude of peaks are affected. The effect is much more noticeable than that of setting P_{lim} to 1, but less than the effect of setting I_{lim} to 1.

315 4. Discussion

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317 4.1 General findings

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319 We stress that the model presented is a highly simplified version of the system. This approach moves
320 away from the trend towards algal population models that are driven by complex functions, and have
321 considerable requirements for site-specific parameter estimates and monitoring data. However, we
322 contend that this simple approach is sufficient for the construction of a policy model designed for algal
323 bloom management. We have shown that the formation of cyanobacterial blooms (at least for this
324 case) can be understood in terms of simple environmental variables, and well-founded physical and
325 biological relationships, and that a model driven by standard monitoring data can largely recapitulate
326 the patterns of the cyanobacterial population over a lengthy period. This latter finding is especially
327 important, as models that are to find broad use for management must be able to be driven by such
328 data sets, despite the fact that they are collected at low spatial and temporal resolution, and that
329 relatively few parameters are monitored.

330

331 The sensitivity analyses showed that of the measured environmental variables, temperature had the
332 greatest effect, and that light limitation was far more important than phosphorus limitation of growth
333 rate. These results are largely in accordance with existing knowledge of the factors that affect blue-
334 green algal populations, and further support the idea that the model is behaving in a sensible manner.
335 Temperature has previously been identified as being important in mediating algal populations in
336 Australia (e.g. Maier, et al., 2001). In Australian systems, light limitation is generally believed to be
337 important (e.g. Bowling and Baker, 1996), and phosphorus is generally thought to be of less
338 importance (e.g. Hötzel and Croome, 1994) than it is elsewhere (e.g. Jacoby, et al., 2000). Flow has
339 generally been identified as an important factor regulating algal populations in Australia (e.g. Maier, et
340 al., 2001), and although it did not feature heavily in the sensitivity analysis, the choice of F_c was found
341 to be important for one of the modelled peaks.

342

4.2 Effects of data quality

As mentioned above, the monitoring data used to drive the model were taken from single near-surface samples collected at irregular intervals. The lack of replication means that there is no estimate of small-scale lateral or vertical spatial variability. It is also obvious that the single sampling location will not be representative of the weir as a whole. Additionally, given that we filled gaps between samples by linear interpolation, we are certain to have missed some temporal changes in conditions. These inaccuracies might be expected to affect model output. However, for the most part, perturbation of the driving data by ±10% did not affect model performance noticeably, and so the quality of the data is less important. The exception to this was the monitored temperature (*Te*). The temperature readings taken at Bourke were from near the water's surface, and do not represent the range of temperatures that will be seen at different depths. Moreover, they are not collected consistently at the same time each day. One would expect this inaccuracy in the data to be important, and better characterisation of field temperatures may improve model performance.

Additionally, the cell counts against which the model was validated were also collected as single near-surface samples. It is certain that cell numbers would have shown great spatial and temporal variability within the weir, and the sampling procedure would not have served to either quantify (e.g. via multiple samples) or reduce (via integration of multiple samples) such variability. Moreover, the sampling error for the cell counts will be great at low densities (Guillard, 1973). For example, Bormans and Condie (1998) assumed a ±100% error for *Anabaena* cell counts of less than 1000 cells mL^{-1}. As a result, it is only once cell numbers start to approach the management threshold of 2000 cells mL^{-1} that the actual counts even start to be representative of the single sample taken. Thus we cannot compare the modelled population to monitoring data at low cell concentrations, which is another reason why testing the model in terms of threshold exceedence is an appropriate validation strategy.

Model performance was noticeably affected by perturbation of a number of model parameters. In reality, the values of model parameters will vary, rather than being a fixed value. Thus it is certain that the values used in this model are, to some extent, "wrong". Of more interest than the effect of fixed

perturbations on model output will be the effect of stochasticising the parameter values during model execution. Work is currently under way on a version of the model that uses such values. Such a model will better be able to determine the effects of perturbing the mean value of a parameter value, and will be able to identify those parameters for which extra work should be performed to better characterise mean and variance in “natural” situations.

4.3 Model performance

It seems certain that there are important factors governing the population that are not being modelled. This contention is supported by the two greatly extended modelled blooms (late 1992, late 2001), and the falsely predicted bloom (late 1997) that occurred. At these points, the model is clearly lacking some important data. For these three cases, an examination of the driving data showed that conditions were similar to those during which other blooms were modelled. For the two greatly extended blooms, the single factor that distinguished them most from the other modelled peaks was that the correctly forecast bloom was not dissipated by a massive and sudden increase in flow rate. Clearly, therefore, there are agents other than flow that can terminate an algal bloom. Such agents could also be used to explain the falsely predicted bloom. We do not know what these agents are, but can speculate upon several possible causes. Research has shown that blooms can be prevented or terminated by predation (e.g. Pechar, 1995) or pathogenesis (e.g. Rashidan and Bird, 2001). The latter is perhaps more likely, as Boon *et al*. (1994) found that Australian zooplankton were unlikely to be able to ingest sufficient cyanobacteria to prevent or terminate blooms. An alternative explanation is that salinity in the weir increased during the extended periods of low flow. Salinity has a toxic effect on cyanobacteria, and has previously been built into algal population models (e.g. Lung and Paerl, 1988) as a source of mortality that changes with EC. However, EC was part of the standard monitoring program at Bourke, and when we examined the data, we did not find any pattern of salinity values that could explain the model’s ‘misbehaviour’. Similarly, the accidental (through irrigation run-off) or deliberate application of pesticides could terminate blooms. However, there are no data to investigate this hypothesis.

401 The sensitivity analysis demonstrated that the height of modelled population peaks was sensitive to
402 several parameters within the model. As such, the fact that modelled peaks did or did not exceed the
403 threshold point was determined at least partly by the combination of parameter values derived from
404 the literature. If sensitive parameters are independent of other parameters, as assumed in the
405 sensitivity analysis, then the output of the model must be viewed with caution, particularly with regards
406 to the exceedence of the management threshold of 2000 cells mL^{-1}. However, we believe that
407 mortality will be correlated with population size. We simply did not have any data to quantify such a
408 relationship in the model. Thus, in the natural system, differences in parameters that increase the rate
409 of population growth would be offset by mortality, and vice versa. As such, the sensitivity analysis as
410 presented is overly conservative, and the magnitude of effects of perturbations is likely to be smaller.
411 However, the sensitivity analysis, together with the above observations makes it clear that the choice
412 of several of the parameter values used in the model was important to achieve the results seen.
413
414 4.4 Model structure and complexity
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416 As stated in the introduction, the goal of this study was to produce a model that was as simple as
417 possible, but still useful from a management perspective. In so doing, we deliberately did not
418 represent many processes as accurately as is made possible by the large amount of work that has
419 been done on cyanobacteria biology and the physical environments that they inhabit.
420
421 Most obviously, perhaps, we modelled the growth – irradiance relationship using a very simple
422 relationship, and also made some gross simplifications concerning the light climate above the water
423 column. As stated above, the 'curve' first postulated by Bannister (1979), has been successfully
424 applied to photosynthesis – irradiance modelling, but a number of other more sophisticated curves
425 exist (Jassby and Platt, 1976). The simple relationship had appeal in that it could be combined with
426 the Beer-Lambert relationship for light attenuation, and was still easily integrated in order to produce
427 the equation for daily I_{lim}. An obvious choice for a more sophisticated growth – irradiance curve in this
428 case would be that of McCausland *et al.* (2002), which was successfully applied to *Anabaena*
429 *circinalis.* However, once this formula is combined with the Beer-Lambert relationship, we are left with

an expression that cannot be integrated using conventional calculus. We produced a version of the model that used this research, and employed numerical integration to calculate growth at any depth / time. Run time of the resulting model was increased by a factor of ~50. However, the extra complexity produced a simulated algal population that was not noticeably different to that produced by the original model. Thus, we decided that the simple model structure was adequate for the task. Such a finding is analogous to that recently reported by Flynn (2003), who tested outputs from complex phytoplankton photoacclimation models to those produced by empirical models that did account for internal processes. He found no substantial differences in output between the two model types, and thus reasoned that there was often no justification for the use of the photoacclimation models in oceanographic phytoplankton simulations.

The formation and breakdown of thermal stratification is another phenomena that was treated very simplistically in this model, and yet has been widely studied. The depth of a mixed layer can be calculated using equations summarised in Reynolds *et al.* (1987). Such equations require data on solar irradiance, air temperature and wind speed. Solar irradiance can be calculated for an environment such as Bourke that experiences little cloud cover. However, data for air temperature and wind speed would have to be sourced. It is worth noting that high banks and stands of River Red Gums shelter the waters of Bourke Weir, and so wind data from a nearby weather station would be inaccurate. Moreover, the relationships employed by the equations mentioned above break down at low wind speeds (Oliver and Ganf, 2000). Lastly, and most importantly for our choice of simple model, studies of similar systems have found that thermal stratification is mainly influenced by flow rate in a weir pool environment (e.g. Sherman, et al., 1998).

The model contains other simple representations of complex functions. Perhaps most obviously, there are no density dependent effects on the population, other than the absolute ceiling on population imposed by available phosphorus. This simplification probably explains why the model tends to overestimate peak population values, and appears to underestimate low population values (although the discussion of the non-reliable nature of low population counts must be borne in mind here). Similarly, we have assumed a fixed phosphorus quota per cell contrary to observed patterns under

459 bloom conditions (Kristov, et al., 1999), and have not allowed for luxury uptake of phosphorus
460 (Cembella, et al., 1984) or growth via internal stores (Droop, 1974). Despite these and other
461 simplifications, the model appears to perform the task for which it was designed. It does not need to
462 be complex in order to do this. As such, this simple model has potential to be useful as a management
463 tool, and appears to be worthy of further research.
464
465 4.5 Further development
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467 Much of the above discussion has centred on application of the model to the test case – *Anabaena* sp.
468 in Bourke Weir. The true utility of this model will become known when it is applied to other situations.
469 The unaltered model is likely to be portable if applied to other weir pools, especially on the Darling
470 River, although it is possible that the combination of parameter values (e.g. r_{20}, q, Q_{10}) that produced
471 good results for Bourke Weir, might not work so well in another environment. In environments where
472 wind might become important in mediating mixing (shallow impoundments or lakes), it is likely to need
473 some modification. Similarly, unlike Bourke, few environments have clear skies for most of the year.
474 For intermittently cloudy environments, some complication of the light limitation routine might be
475 inevitable. Given the overwhelming importance of light limitation in the Bourke Weir system, we do not
476 know how well the model might work in a nutrient limited system. Similarly, how well this model might
477 work for other dominant cyanobacterial species is unknown at this stage.
478
479 Finally, to use this model in a predictive sense, the driving data need to be predicted. By keeping the
480 number of data types required to a minimum, we increase the ease with which driving data can be
481 predicted. Although it is pure speculation at this stage, it may be possible to use climate models to
482 produce simulations of flow and temperature, and then use empirical models to predict phosphorus
483 and turbidity from the flow data. The incorporation of stochastic elements into the data predictions, and
484 into the model itself would then allow it to be used to assess the risks of algal blooms in the future
485 under different year to year climate scenarios.
486

5. Conclusions

We have shown that a relatively simple process-based model can be used to model the occurrence of blooms of *Anabaena* sp. in Bourke Weir. The model was driven by standard monitoring data, and processes were modelled based on existing research. While the model could not accurately predict cell numbers in the weir, it could predict the onset of blooms, and this is of primary importance to water resource managers. The model did falsely predict one bloom, but more importantly, it did not fail to predict any of the blooms that occurred between 1992 and 2002. This performance occurred despite the model using simplifications of a number of processes. Such simplifications greatly reduced model complexity, increasing the chances that the model will be portable between sites, and may find use as a management tool.

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505 Bibliography

506

507 Bannister, T.T., 1979. Quantitative description of steady state, nutrient-saturated algal growth,
508 including adaptation. Limnol. Oceanogr., 24: 76-96.
509 Beasley, V.R., Cook, W.O., Dahlem, A.M., Hooser, S.B., Lovell, R.A. and Valentine, W.M., 1989.
510 Algae intoxication in livestock and waterfowl. Vet. Clin. N. Am.-Food Anim. Pract., 5: 345-361.
511 Belov, A.P. and Giles, J.D., 1997. Dynamical model of buoyant cyanobacteria. Hydrobiologia, 349: 87-
512 97.
513 BGATF, 1992. Blue-Green Algae: Final Report of the New South Wales Blue-Green Algal Task Force.
514 Department of Water Resources, Parramatta, 159 pp.
515 Boon, P.I., Bunn, S.E., Green, J.D. and Shiel, R.J., 1994. Consumption of cyanobacteria by freshwater
516 zooplankton: Implications for the success of 'top-down' control of cyanobacterial blooms in
517 Australia. Aust. J. Mar. Freshw. Res., 45: 875-887.
518 Bormans, M. and Condie, S.A., 1998. Modelling the distribution of *Anabaena* and *Melosira* in a
519 stratified weir pool. Hydrobiologia, 364: 3-13.
520 Bowling, L.C. and Baker, P.D., 1996. Major cyanobacterial bloom in the Barwon-Darling River,
521 Australia, in 1991, and underlying limnological conditions. Mar. Freshw. Res., 47: 643-657.
522 Bowling, L.C., Cullen, P., Green, J., Hart, B., McKay, G., Oliver, R., Shiel, R. and Wasson, B., 1991.
523 Darling River Scientific Advisory Team, Initial Report, December 23, 1991. Blue-Green Algae:
524 Final Report of the New South Wales Blue-Green Algal Task Force. Department of Water
525 Resources, Parramatta, Appendix I.
526 Cembella, A.D., Anita, N.J. and Harrison, P.J., 1984. The utilisation of inorganic and organic
527 phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective:
528 part 1. In: CRC Critical Reviews in Microbiology. Vol. 10, pp. 317-391.
529 Dillon, P.J. and Rigler, F.H., 1974. The phosphorus - chlorophyll relationships in lakes. Limnol.
530 Oceanogr., 19: 767-773.
531 Droop, M.R., 1974. The nutrient status of algal cells in continuous culture. J. Mar. Biol. Assoc. U.K.,
532 54: 825-855.

533 Easthope, M.P. and Howard, A., 1999. Simulating cyanobacterial growth in a lowland reservoir. Sci.
534 Total Environ., 241: 17-25.
535 Everbecq, E., Gosselain, V., Viroux, L. and Descy, J.-P., 2001. POTAMON: a dynamic model for
536 predicting phytoplankton composition and biomass in lowland rivers. Water Res., 35: 901-912.
537 Flynn, K.J., 2003. Do we need complex mechanistic photoacclimation models for phytoplankton?
538 Limnol. Oceanogr., 48: 2243-2249.
539 French, M. and Recknagel, F., 1994. Modelling of algal blooms in freshwaters using artificial neural
540 networks. In: P. Zanetti (ed.) Computer Techniques in Environmental Studies V. Vol II.
541 Environmental Systems, Computational Mechanics Publications, Boston, pp. 87-94.
542 GBCMA, 2003. Goulburn Broken Water Quality Strategy 1996-2016. Goulburn Broken Catchment
543 Management Authority, Shepparton, 160 pp.
544 Guillard, R.R.L., 1973. Division rates. In: J.R. Stein (ed.) Handbook of Phycological Methods. Culture
545 Methods and Growth Measurements. Vol. 1, Cambridge University Press, New York, pp. 289-
546 311.
547 Healey, F.P., 1973. Characteristics of phosphorus deficiency in *Anabaena*. J. Phycol., 9: 383-394.
548 Hötzel, G. and Croome, R., 1994. Long-term phytoplankton monitoring of the Darling River at
549 Burtundy, New South Wales: Incidence and significance of cyanobacterial blooms. Aust. J.
550 Mar. Freshw. Res., 45: 747-759.
551 Howard, A., Kirby, M.J., Kneale, P.E. and McDonald, A.T., 1995. Modelling the growth of
552 cyanobacteria (GrowSCUM). Hydrol. Process., 9: 809-820.
553 Jacoby, J.M., Collier, D.C., Welch, E.B., Hardy, F.J. and Crayton, M., 2000. Environmental factors
554 associated with a toxic bloom of *Microcystis aeruginosa*. Can. J. Fish. Aquat. Sci., 57: 231-
555 240.
556 Jassby, A.D. and Goldman, C.R., 1974. Loss rates from a lake phytoplankton community. Limnol.
557 Oceanogr., 19: 618-627.
558 Jassby, A.D. and Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis
559 and light for phytoplankton. Limnol. Oceanogr., 21: 540-547.
560 Jochimsen, E.M., Charmichael, W.W., An, J.S., Cardo, D.M., Cookson, S.T., Christianne, M.D.,
561 Holmes, E.M., de Antunes, M.B.C., de Melo Filho, D.A., Lyra, T.M., Barreto, V.S.T., Azevedo,

562 S.M.F.O. and Jarvis, W.R., 1998. Liver failure and death after exposure to microcystins at a
563 hemodialysis center in Brazil. N. Engl. J. Med., 338: 873-878.
564 Jones, G.J. and Orr, P.T., 2000. Development of a toxic cyanobacteria management plan for Southern
565 Rural Water, Victoria. Stage 1: water usage risks, water storage vulnerability, advisory levels,
566 and best practices. CSIRO Land and Water, Indooroopilly, 62 pp.
567 Kirk, J.T.O., 1994. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press,
568 Cambridge, 509 pp.
569 Kneale, P.E. and Howland, A., 1997. Statistical analysis of algal and water quality data. Hydrobiologia,
570 349: 59-63.
571 Kristov, V., Bellinger, E.G. and Sigee, D.C., 1999. Modelling of elemental associations in *Anabaena*.
572 Hydrobiologia, 414: 77-83.
573 Laws, E.A. and Chalup, M.S., 1990. A microalgal growth model. Limnol. Oceanogr., 35: 597-608.
574 Lewis, D.M., Elliott, J.A., Lambert, M.F. and Reynolds, C.S., 2002. The simulation of an Australian
575 reservoir using a phytoplankton community model: PROTECH. Ecol. Model., 150: 107-116.
576 Lung, W.-S. and Paerl, H.W., 1988. Modeling blue-green algal blooms in the lower Neuse River. Water
577 Res., 22: 895-905.
578 Maier, H.R., Sayed, T. and Lence, B.J., 2001. Forecasting cyanobacterium *Anabaena* spp. in the
579 River Murray, South Australia, using B-spline neurofuzzy models. Ecol. Model., 146: 85-96.
580 McCausland, M.A., Thompson, P.A. and Blackburn, S.I., 2002. The effect of changes in light
581 availability caused by mixing on the growth of *Anabaena circinalis* (Nostocales,
582 Cyanobacteria) and *Aulacoseria* sp. (Centrales, Bacillariophyceae). Phycologia, 40: 530-541.
583 McIntosh, B.S., 2003. Qualitative modelling with imprecise ecological knowledge: a framework for
584 simulation. Environ. Modell. Softw., 18: 295-307.
585 Mitrovic, S. and Gordon, A., 1998. Barwon-Darling Riverwatch: algae and water quality report 1992-
586 1997. Report No. CNR 98.010. Department of Land and Water Conservation - Centre for
587 Natural Resources, Sydney, 116 pp.
588 Mitrovic, S.M., Oliver, R.L., Rees, C., Bowling, L.C. and Buckney, R.T., 2003. Critical flow velocities for
589 the growth and dominance of *Anabaena circinalis* in some turbid freshwater rivers. Freshw.
590 Biol., 48: 164-174.

591 Nalewajko, C. and Lean, D.R.S., 1980. Phosphorus. In: I. Morris (ed.) The Physiological Ecology of
592 Phytoplankton, Blackwell Scientific, Ann Arbor, Michigan, pp. 235-258.
593 Oliver, R.L. and Ganf, G.G., 2000. Freshwater blooms. In: B.A. Whitton and M. Potts (eds.), The
594 Ecology of Cyanobacteria, Kluwer Academic Publishers, Dordrecht, pp. 149-194.
595 Oliver, R.L., Hart, B.T., Olley, J., Grace, M., Rees, C. and Caitcheon, G., 1999. The Darling River:
596 Algal growth and cycling and sources of nutrients. Report No. M386. Cooperative Research
597 Centre for Freshwater Ecology and CSIRO Land and Water, Canberra.
598 Paerl, H.W., 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. Limnol.
599 Oceanogr., 33: 823-847.
600 Pechar, L., 1995. Long-term changes in fish pond management as an unplanned ecosystem
601 experiment - importance of zooplankton structure, nutrient and light for species composition of
602 cyanobacterial blooms. Water Sci. Technol., 32: 187-196.
603 Rashidan, K.K. and Bird, D.F., 2001. Role of predatory bacteria in the termination of a cyanobacterial
604 bloom. Microb. Ecol., 41: 97-105.
605 Reynolds, C.S., Oliver, R.L. and Walsby, A.E., 1987. Cyanobacterial dominance: the role of buoyancy
606 regulation in dynamic lake environments. N. Z. J. Mar. Freshw. Res., 21: 379-390.
607 Reynolds, C.S., Irish, A.E. and Elliott, J.A., 2001. The ecological basis for simulating phytoplankton
608 responses to environmental change (PROTECH). Ecol. Model., 140: 271-291.
609 Scheffer, M. and Beets, J., 1994. Ecological models and pitfalls of causality. Hydrobiologia, 275/276:
610 115-124.
611 Sherman, B.S., Webster, I.T., Jones, G.J. and Oliver, R.L., 1998. Transitions between *Aulacoseira* and
612 *Anabaena* dominance in a turbid river weir pool. Limnol. Oceanogr., 43: 1902-1915.
613 Smith, V.H., Tilman, G.D. and Nekola, J.C., 1999. Eutrophication: impacts of excess nutrient inputs on
614 freshwater, marine, and terrestrial ecosystems. Environ. Pollut., 100: 179-196.
615 Steel, J.A., 1997. Scope and limitation in algal modelling - an example from the Thames Valley
616 reservoirs. Hydrobiologia, 349: 27-37.
617 Thompson, P.-A., Oh, H.-M. and Rhee, G.-Y., 1994. Storage of phosphorus in nitrogen-fixing
618 *Anabaena flos-aquae* (Cyanophyceae). J. Phycol., 30: 267-273.

619 Walker, C. and Greer, L., 1992. The economic costs associated with lost recreation benefits due to
620 blue-green algae in New South Wales: three case studies. Blue-Green Algae: Final Report of
621 the New South Wales Blue-Green Algal Task Force. Department of Water Resources,
622 Parramatta, Appendix F.
623 Whitehead, P.G. and Hornberger, G.M., 1984. Modelling algal behaviour in the River Thames. Water
624 Res., 18: 945-953.
625 Whitton, B.A. and Potts, M., 2000. Introduction to the Cyanobacteria. In: B.A. Whitton and M. Potts
626 (eds.), The Ecology of Cyanobacteria, Kluwer Academic Publishers, Dordrecht, pp. 1-11.
627 Yabunaka, K., Hosomi, M. and Murakami, A., 1997. Novel application of a back-propagation artificial
628 neural network model formulated to predict algal bloom. Water Sci. Technol., 36: 89-97.
629 Yu, S.-Z., 1994. Blue-green algae and liver cancer. In: D.A. Steffensen and B.C. Nicholson (eds.),
630 Toxic Cyanobacteria: Current Status of Research and Management - Proceedings of an
631 International Workshop, Australian Centre for Water Quality Research, Adelaide, pp. 75-85.
632
633

633 Table I. Values of process parameters used in the model, and sources from which they were drawn.

634

Parameter	Description	Value	Source
N_μ	Mean Day Length	12 h	Estimate
N_r	Range of Day Length	4 h	Estimate
Z_e	Mixing depth when weir is stratified	0.75 m	Oliver *et al*. (1999), Mitrovic *et al*. (2003)[a]
F_c	Flow out of the weir that leads to stratification	800 ML d^{-1}	Oliver *et al*. (1999)[b]
Z_w	Weir Depth	4.5 m	Oliver *et al*. (1999)
W_w	Weir Width	60 m	Oliver *et al*. (1999)
L_w	Weir Length	40 km	Oliver *et al*. (1999)
I_{sat}	Illumination required to saturate growth rate	$0.15 \cdot I_0$	McCausland *et al.* (2002), Kirk (1994)[c]
V_w	Weir Volume	4500 ML	Oliver *et al*. (1999)
P_{cell}	Phosphorus Quota of one *Anabaena* cell	$1.42 \cdot 10^{-8}$ µmol	Thompson *et al*. (1994)
P_{spm}	Phosphorus tightly bound to sediments	17.1 µmol g^{-1}	Grace (unpubl.)
K_S	Half saturation coefficient of P uptake	0.21 µmol L^{-1}	Nalewajko and Lean (1980), Cembella *et al*. (1984)[d]
Q_{10}	Proportional increase in growth rate with a 10°C increase	2.1	Healey (1973)
q	Mortality	0.3 d^{-1}	Jassby and Goldman (1974)[e]
cA_{wi}	Algal cell concentration in water entering weir	1 mL^{-1}	Small nominal value
r_{20}	Population growth rate at 20°C	0.58 d^{-1}	McCausland *et al*. (2002)[f]

[a] Both studies describe an initial mixing layer as being from 0.5 to 1.0 m thick. Took average.
[b] 800-1000 ML d^{-1} appears to promote persistent stratification. Took low end after Mitrovic *et al.* (2003) reported 450 ML d^{-1} required to cause persistent stratification (contradicts observations in this data set).
[c] The figure was calculated by i) taking the light intensity at which growth of *Anabaena circinalis* was maximised in McCausland *et al.* (2002), and ii) dividing it by the average surface irradiance for Bourke during the 'bloom season' November – March. We calculated surface irradiance using the methods published in Kirk (1994), and by assuming 80% transmission of radiation through the usually clear skies at Bourke and 45% for the percentage of radiation reaching the surface as photosynthetically active radiation.
[d] Calculated as the average of figures given for natural algal assemblages, with each independent study counting as one data point. Laboratory studies of individual species have generally reported K_S that are much lower than estimates for assemblages in the field (Nalewajko and Lean, 1980, Cembella, et al., 1984). Consequently we decided against using a laboratory estimate of K_S for *Anabaena*.
[e] Average loss rate for the months of maximal production (July-August) – data points calculated from graph.
[f] McCausland *et al.* (2002) present growth rates for flask cultures and for tanks designed to mimic field illumination and mixing conditions. The figure is the average for 'field mimic' growth rates (growth rate units converted from ln to $\log_2$ – doublings per day, and scaled to account for 14 h maximum day length).

635

636

636 Table II. Results of the sensitivity analysis. Table shows effect on model output of perturbing each of
637 the numerical parameters by ±10%, in terms of the percentage of days re-classified as being over or
638 under the management threshold of 2000 cells mL^{-1}. Parameters are ranked by average effect size.
639

Perturbation ⇒	**+10%**	**-10%**	**Perturbation ⇒**	**+10%**	**-10%**
Parameter altered	**Change %**		**Parameter altered**	**Change %**	
Te	3.5	3.6	P_{tot}	0.1	0.3
r_{20}	2.2	2.4	N_{μ}	0.1	0.2
q	2.1	1.6	Intercept 0.73 (eq. 4)	0.2	0.1
Q_{10}	1.1	0.9	cA_{wi}	0.1	0.2
F_c	0.5	0.9	K_S	0.2	0.1
F	0.8	0.5	V_w	0.1	0.1
Tu	0.7	0.4	L_w	0.1	0.0
Slope 0.04 (eq. 4)	0.7	0.4	P_{cell}	0.1	0.0
Z_e	0.5	0.4	W_w	0.1	0.0
Z_w	0.4	0.2	Slope 0.67 (eq. 7)	0.0	0.0
I_{sat}	0.3	0.2	Intercept 52 (eq. 7)	0.0	0.0
N_r	0.2	0.2	P_{spm}	0.0	0.0

640
641

641 Figure Captions

642

643 Figure 1. Map showing the location of Bourke Weir in northern NSW, Australia, and the gauging
644 station from which data were collected.

645

646 Figure 2. Conceptual model upon which the numerical model of *Anabaena* populations was based.

647

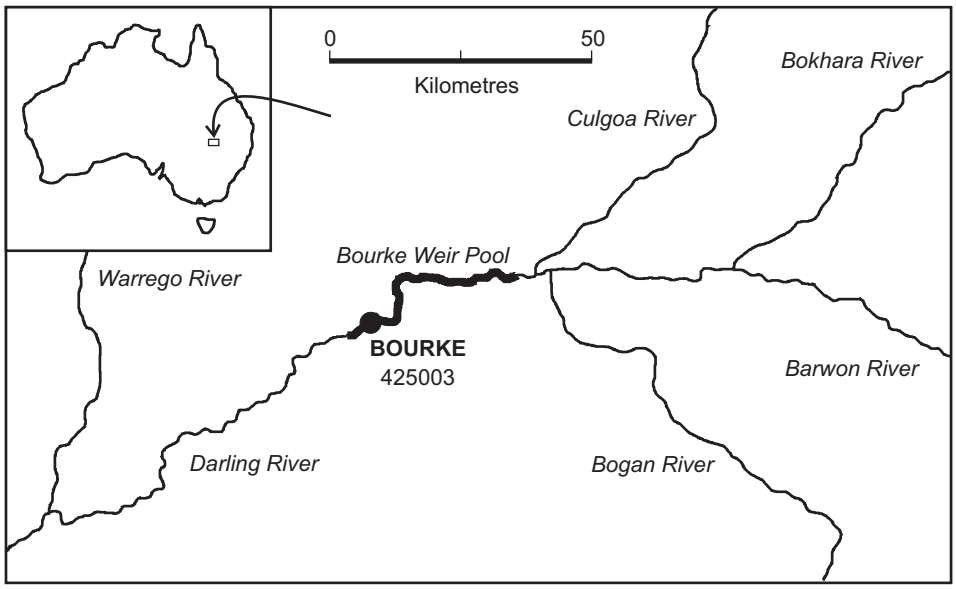
648 Figure 3. Model performance. The graph shows monitored concentrations of cyanobacteria in Bourke
649 Weir for the period 1992-2002 (circles) and the population of *Anabaena circinalis* as projected by the
650 model (line). The horizontal dashed line shows the management threshold of. 2000 cells mL^{-1}. X-axis
651 shows time, and Y-axis shows cell concentration (mL^{-1}) + 1 on a log scale

652

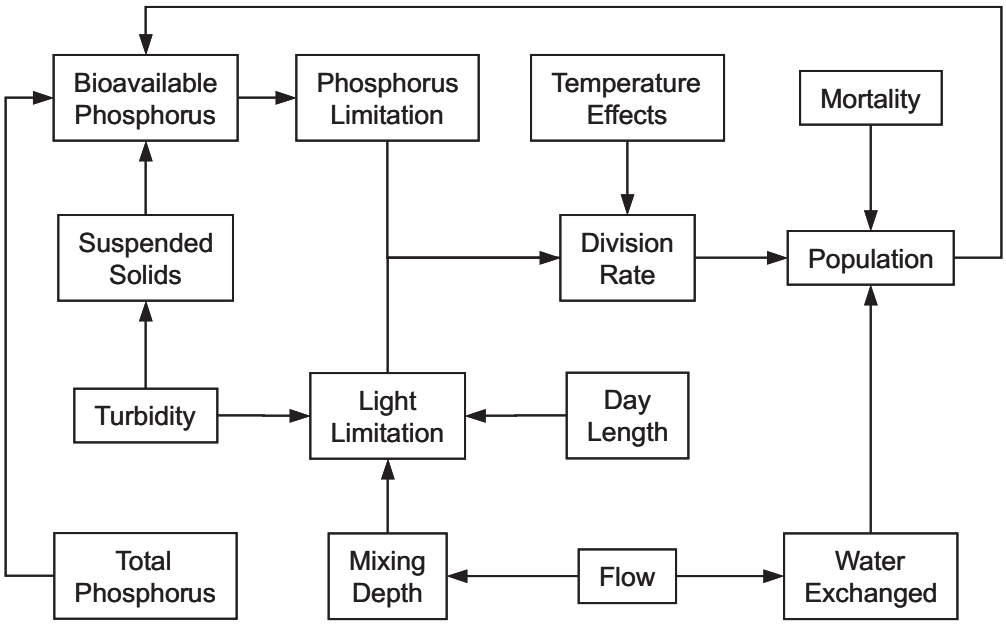
653 Figure 4. Results of the sensitivity analysis for the five most sensitive parameters. The two lines show
654 the population as modelled with the +10% and -10% perturbations, respectively. The filled area
655 highlights the degree of divergence between the two modelled populations at any point in time. The
656 circles mark the heights reached by population peaks in the unperturbed model.

657

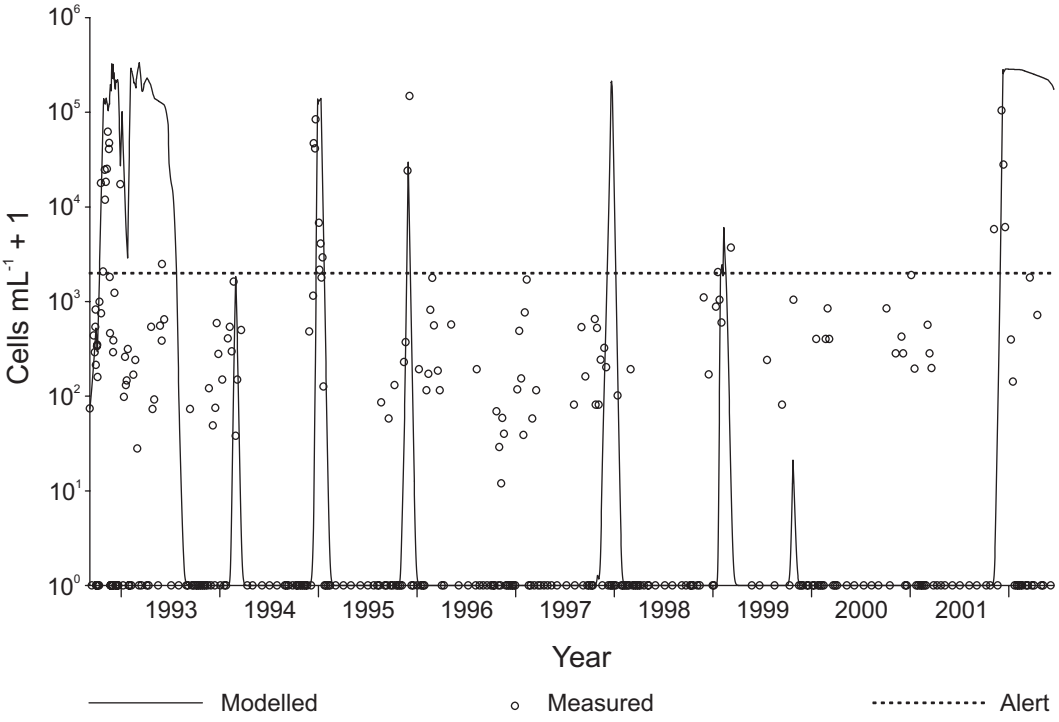
658 Figure 5. Effect of setting limiting scalars to 1. The three graphs show the original modelled population
659 (solid line) compared to populations in which I_{lim}, P_{lim}, and S_{Te} were set to 1, respectively (dashed line).



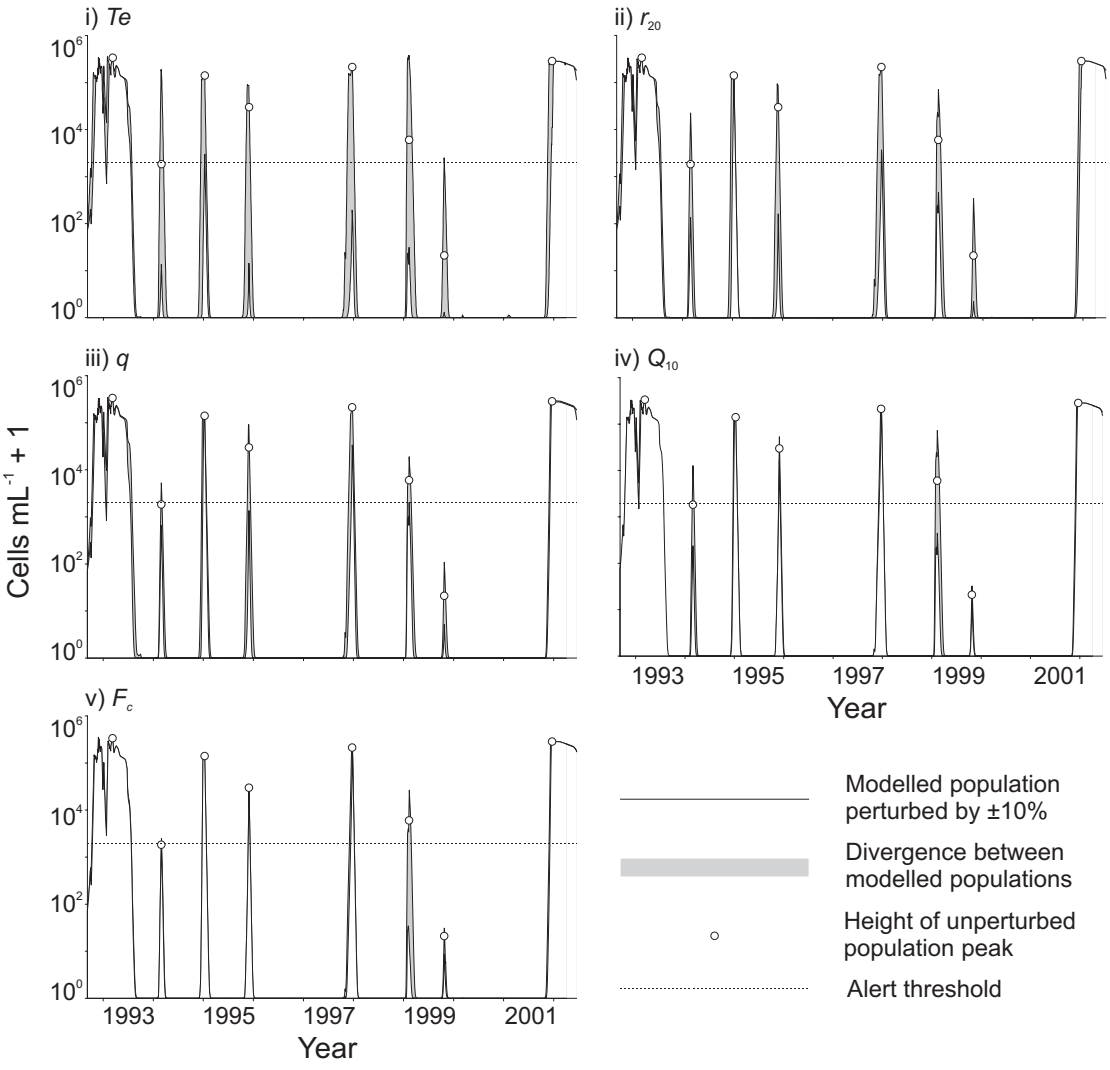
Webb et al. Figure 1



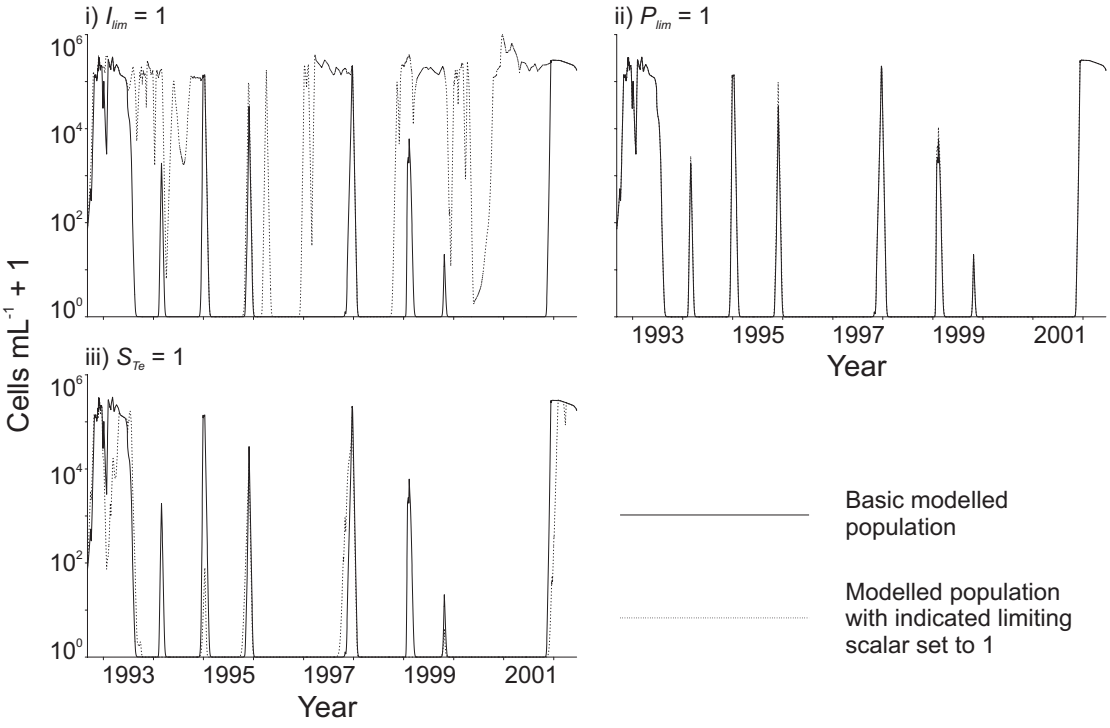
Webb et al. Figure 2



Webb et al. Figure 3



Webb et al. Figure 4



Webb et al. Figure 5