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Advancing projections of phytoplankton responses to climate change through ensemble modelling

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Abstract

A global trend of increasing health hazards associated with proliferation of toxin-producing cyanobacteria makes the ability to project phytoplankton dynamics of paramount importance. Whilst ensemble (multi-)modelling approaches have been used for a number of years to improve the robustness of weather forecasts this approach has until now never been adopted for ecosystem modelling. We show that the average simulated phytoplankton biomass derived from three different aquatic ecosystem models is generally superior to any of the three individual models in describing observed phytoplankton biomass in a typical temperate lake ecosystem, and we simulate a series of climate change projections. While this is the first multi-model ensemble approach applied for some of the most complex aquatic ecosystem models available, we consider it sets a precedent for what will become commonplace methodology in the future, as it enables increased robustness of model projections, and scenario uncertainty estimation due to differences in model structures.

1. Introduction

Ecological processes in lakes and reservoirs are highly sensitive to environmental change (Williamson et al., 2008). Phytoplankton, being an integral component of lake food webs, has proven to be particularly responsive to changes in factors influenced by global change such as nutrients (Reynolds, 1984; Lampert and Sommer, 1997) and climate (Huber et al., 2008; Jöhnk et al., 2008). This sensitivity is of particular concern to lake managers around the world and, when coupled with the related health hazard of cyanobacterial blooms (Chorus and Bartram, 1999; Paerl and Huisman, 2008), makes understanding their ecology and projecting their biomass of paramount importance.

Projecting cyanobacterial blooms has proved challenging and has motivated the development of numerous computer models that have attempted to simulate the seasonal development of lake phytoplankton (Mooij et al., 2010; Trolle et al., 2012). Nevertheless, with the additional pressures that freshwater ecosystems are subject to with a changing climate, the need for the predictive ability of such models has never been more important than now (Dale et al., 2006; Oliver et al., 2012). However, most studies that simulate future impacts on lake phytoplankton have utilised only a single mechanistic model (Mooij et al., 2007; Trolle et al., 2011; Elliott, 2012). Whilst such studies have merit, the advantage of applying multiple, independently developed models - i.e., an ensemble modelling approach - to a given lake system is that some of the inherent uncertainties in the individual model projections can be reduced by conveying the mean and range of the projections. Nevertheless, no ensemble modelling studies have yet been carried out for projection of lake phytoplankton dynamics, perhaps due to constraints associated with both the considerable resources and the availability of expertise needed to model these aquatic ecosystems.

In this study we take advantage of the expertise available within an international network of modelling experts and apply three autonomously developed models to the same freshwater lake system. We do not intend to provide a comprehensive review of the conceptual differences between these models (for that, we refer to the bulk of literature already available, e.g., Mooij et al., 2010 and Trolle et al., 2012), but rather take advantage of these differences in evaluating the diversity of simulated signals they provide. We further simulate a range of future climate change scenarios, represented by a 1.5, 3 and 5 ℃ warming scenario and two increased nutrient load scenarios, so that the different model projections and likely impacts of warming can be assessed. We test our hypothesis that, as for weather forecast models, the ensemble model mean (derived as the daily average of output from the three individual models) can provide a better predictive working model compared with any individual model (Gneiting and Raftery, 2005.), whilst also allowing statistical uncertainties to be expressed where otherwise they would not be, i.e., with the more common approach of applying a single mechanistic model. We test this method on Lake Engelsholm (Denmark) which, like many other lowland lakes worldwide, has been undergoing eutrophication as a result of decades of anthropogenic impacts from both point and diffuse sources of nutrient pollution.

2. Methods

2.1. Study site

Lake Engelsholm is a typical small (surface area of 0.44 km^2) and shallow (maximum depth of 6.1 m, mean depth of 2.4 m) lake in Denmark. It is currently in a eutrophic state caused by high external nutrient loads from the surrounding catchment, resulting in an annual average Secchi depth of approx. 2 m, annual average chlorophyll *a* concentrations of approx. 25-30 mg m^{-3} (data from 1999-2001), and occasional occurrences of cyanobacterial blooms during summers. The catchment area (15.2 km^2) consists mainly of cultivated areas (78 %, predominantly arable land), forested hills (16 %) and scattered dwellings (6 %).

2.2. Model applications

The three models used in this study were DYRESM-CAEDYM (Hamilton and Schladow, 1997), PROTECH (Elliott et al., 2010) and PCLake (Janse, 1997). Each individual model is applied as it would be typically for a small temperate lake, and thus the configuration of the conceptual ecosystem is allowed to vary between models, reflecting how each of the three models has typically been applied in previous studies. DYRESM-CAEDYM (DYCD) is a one-dimensional ecological model consisting of two main components: a one-dimensional hydrodynamic model (DYRESM: Dynamic Reservoir Simulation Model), which resolves vertical mixing and the resulting distribution of temperature, salinity and density in a lake/reservoir, and an aquatic ecosystem model (CAEDYM: Computational Aquatic Ecosystem Dynamics Model), which simulates a range of biological and chemical variables, such as inorganic and organic forms of phosphorus and nitrogen, up to seven phytoplankton groups/species and up to five zooplankton groups/species (Trolle et al., 2008). If a lake is characterized by a complex bathymetry, and higher spatial resolution is required due to the importance of horizontal circulation and transport processes, CAEDYM can also be run in three dimensions, by coupling to the Estuary, Lake and Coastal Ocean model (ELCOM, a 3-D-structured grid hydrodynamic model). In either 1-D or 3-D studies, the model has been applied in around 70 peer reviewed studies (Trolle et al., 2012), and has typically been used to analyse the effects of changed nutrient loads (Hamilton, 1999) or climate (De Stasio et al., 1996) on lake ecosystem dynamics. In this model the daily change in the phytoplankton biomass in a water column layer ($\Delta X/\Delta t$) attributable to each phytoplankton group is determined by:

$$\Delta X/\Delta t = (r' - R - S - G) X + RS + M - D \qquad (1)$$

where r' is the actual growth rate, R is the accumulated loss due to respiration, mortality and excretion, S is the loss due to settling, G is the loss due to grazing (grazing preferences on each phytoplankton group can be specified for individual zooplankton groups), RS is a gain due to resuspension of phytoplankton biomass from the bottom sediments, M (optional) is the gain or loss from active movement of phytoplankton from or

to neighbouring water layers and D is the loss due to dilution (Hipsey et al., 2007). The actual growth rate (r') is determined from:

$$r' = \mu_{max} \min\{\ f(I),\ f(N),\ f(P),\ f(Si)\ \}\ f(T) \qquad (2)$$

where μ_{max} is the maximum growth rate at 20 °C in the absence of significant limitation by light or nutrients, f(I), f(N) and f(P) represent limitation by light, nitrogen and phosphorus respectively, and f(T) is a temperature function. The f(Si) function represents limitation by silica and applies only to diatoms. The nutrient limitation can be modelled either through a simple Michaelis-Menten expression based on water column concentrations or a dynamic intracellular nutrient store to regulate growth according to the nutrient storage and the water column nutrient concentrations. In the configuration of the conceptual model for DYRESM-CAEDYM in the present study, a total of three phytoplankton groups (representing diatoms, cyanobacteria and dinoflagellates), and two zooplankton groups (representing cladocerans and copepods, respectively) was used. Fish and macrophytes were not included.

PROTECH (Phytoplankton RespOnses To Environmental CHange) simulates the responses of up to 10 species of lake phytoplankton to annual and seasonal changes. It has been applied in over 30 peer reviewed studies (Elliott et al., 2010). A detailed description of the model's equations and concepts has been published (Reynolds et al., 2001; Elliott et al., 2010) and the biological component of PROTECH can be summarised through the daily change in the chlorophyll *a* concentration ($\Delta X/\Delta t$) attributable to each phytoplankton taxon:

$$\Delta X/\Delta t = (r' - S - G - D)\ X + M \qquad (3)$$

where r' is the growth rate defined as a proportional increase over 24 h, S is the relative loss due to settling out from the water column, G is relative the loss due to *Daphnia* grazing (phytoplankton > 50 μm diameter are not grazed (Burns, 1969)), D is the relative loss due to dilution and M is the relative gain from active movement (optional) of phytoplankton from bottom water layers. The growth rate (r') is further defined by:

$$r' = \min\{r'_{(\theta,I)},\ r'_{P},\ r'_{N},\ r'_{Si}\} \qquad (4)$$

where $r'_{(\theta,I)}$ is the growth rate due to temperature and daily photoperiod and r'_{P}, r'_{N}, r'_{Si} are the growth rates determined by phosphorus, nitrogen and silicon if respective concentrations of those nutrients are < 3, 80 and

500 mg m^{-3}, respectively (Reynolds, 2006). The r' values are phytoplankton-dependent (e.g. non-diatom taxa are not limited by silica concentrations below 500 mg m^{-3} and nitrogen-fixing cyanobacteria are not limited by nitrogen) and also relate to the morphology of the taxon (for r'(θ,I)). Temperature and light are varied at each time-step throughout the simulated water-column. For each algal taxon within the model, the value of $\Delta X/\Delta t$ (Equation 4) is modified on a daily time-step for each algal taxon in each layer of the water column. In the configuration of the conceptual model for PROTECH in the present study, a total of eight phytoplankton groups were used (three cyanobacteria, two diatoms, two chlorophytes and one cryptophyte), while zooplankton was implemented by a mortality rate function for phytoplankton based on size selective *Daphina* grazing.

PCLake is an integrated ecological model developed for shallow non-stratifying lakes. It describes phytoplankton, macrophytes and a simplified food web, within the framework of a closed nutrient cycle (Janse et al., 2008; Mooij et al., 2010). The model has been used in approximately 15-20 peer reviewed studies (Trolle et al., 2012). PCLake is designed to provide a representation of organic and inorganic forms of nitrogen and phosphorus, and the interactions between up to three phytoplankton groups, one zooplankton and one zoobenthos group, planktivorous fish (sub-divided into adults and juveniles), piscivorous fish and submerged macrophytes, all within a fully mixed water column. The model is able to analyse the probability of transition between a macrophyte-dominated clear-water state and a phytoplankton-dominated turbid state. The daily change in phytoplankton biomass ($\Delta X/\Delta t$) of each phytoplankton group is determined by:

$$\Delta X/\Delta t = (r' - R - S - G) X + RS - D \qquad (5)$$

where r' is the actual growth rate, R is the accumulated loss due to respiration, mortality and excretion, S is the loss due to settling out of the water column, G is the loss due to zooplankton grazing (preference factors can be specified for individual phytoplankton groups), RS is the gain due to resuspension of phytoplankton biomass from the bottom sediments, and D is the loss due to dilution (or gain if phytoplankton biomass is supplied from inflow boundary). The actual growth rate (r', d^{-1}) is defined by:

$$r' = \mu_{max} \min\{ f(N), f(P), f(Si) \} f(I)\ f(T) \qquad (6)$$

where μ_{max} (day^{-1}) is the maximum growth rate at 20 °C in the absence of significant limitation by light or nutrients, f(I), f(N) and f(P) represent limitation by light, nitrogen and phosphorus respectively, and f(T) is a temperature function. The f(Si) function represents limitation by silica and applies only to diatoms. The nutrient limitation is modelled by inclusion of a dynamic intracellular nutrient store, described through the Droop equation (Riegman and Mur 1984). In the configuration of the conceptual model for PCLake in the present study, a total of three phytoplankton groups (representing diatoms, cyanobacteria and chlorophytes), one zooplankton group, one zoobenthos group, submerged macrophytes, planktivorous/benthivorous fish (subdivided into a juvenile and adult group) and piscivorous fish were used (representing the default state variables for a PCLake application).

2.3. Calibration and validation of phytoplankton dynamics

A two-year (1999-2000) calibration and one-year (2001) validation period were used for all three models. As DYRESM-CAEDYM is the most sophisticated of the models at capturing the vertical variation in thermal structure (and PCLake do not include thermodynamics but need a user-defined temperature forcing), it was set up to derive water column temperatures for input to PROTECH and PCLake. Thus, temperature output generated by DYRESM-CAEDYM was processed and used also by PROTECH and PCLake in both the baseline calibration/validation and in the future scenarios. To calculate the vertical distribution of temperature, DYRESM-CAEDYM requires daily average input data for six meteorological variables, including air temperature (°C), short-wave radiation (W m^{-2}), cloud cover (fraction of whole sky) or long-wave radiation (W m^{-2}), vapour pressure (hPa), wind speed (m s^{-1}) and rainfall (m d^{-1}). These data were acquired from 10-20 km national grids derived from meteorological stations across Denmark and were specified for the Lake Engelsholm location. DYRESM-CAEDYM was very good at reproducing water temperatures, which were used as forcing data in the three ecological models ($r^2 = 0.97$, between observed and simulated temperatures for the 1999-2001 period). Daily inflow and outflow data are also required as boundary conditions for the three models. When continuous flow data were not available, linear interpolation between monthly samples for flow and nutrient concentrations was used to derive daily values within the period 1990-2001. Inflows from any ungauged part of the catchment and from groundwater seepage were

included in a residual term derived from a water balance using measured inflow, outflow, precipitation and estimated evaporation, and assuming constant water level.

To minimize the uncertainty caused by state variable initialization for calibration runs as well as scenarios, the period 1990-1998 was used as a warm-up period (and model output was excluded for evaluation for this period), after which the models were calibrated against observed phytoplankton biomass (represented by total chlorophyll *a*) for years 1999 and 2000. Here, the warm-up simulation period was run using the calibrated model parameters, but disregarded when deriving model performance statistics, which was only done for the period 1999-2000. Model validation of the ability to reproduce observed phytoplankton biomass was subsequently performed on a separate dataset from the year 2001. Model performance during the validation was derived both including and excluding a very high outlier of observed phytoplankton biomass during autumn 2001 (this high value is somewhat uncommon, and could be a localized effect, and thus not representative as a whole lake surface average).

Many model performance metrics exist, and in view of the weaknesses of individual metrics, several of these are ideally used in combination when evaluating model performance (Bennett et al., 2013). We used the coefficient of determination (r^2) and the mean relative absolute error in percent (referred to as MARE by Bennett et al. (2013) and as RE by Arhonditsis and Brett (2004)) to evaluate the goodness of fit to observed phytoplankton biomass data for the three individual models and their ensemble mean derived from the average of daily output of phytoplankton biomass from all three models. We acknowledge that r^2 can suffer significant offset errors (and is differentially sensitivity towards high/extreme values), and therefore we pair r^2 with RE, which provides an indication of overall model bias without the effects of negative biases cancelling out positive biases (Bennett et al., 2013). Using r^2 and RE as performance metrics enables direct comparison to the performances achieved in the 153 individual aquatic biogeochemical modelling studies reviewed by Arhonditsis and Brett (2004).

Observed chlorophyll *a* data (derived from pooled samples from epilimnion) were available at monthly to biweekly intervals throughout the calibration and validation periods. Calibration of phytoplankton dynamics in DYRESM-CAEDYM was done mainly by modifications to the internal supply of nutrients, using release rates of nutrients from the bottom sediments, and parameters relating to intracellular nutrient stores, maximum potential growth rates for phytoplankton and zooplankton grazing rates. For PROTECH, the only modification during calibration was to adjust the release of SRP (soluble reactive phosphorus) from the bottom sediments. PROTECH does not simulate this process directly, but information on it can be entered through the addition of SRP to the water column during certain periods of the year. Therefore, through an iterative calibration process, a value of 2.4 mg SRP m^{-3} was required to be added to the water column in PROTECH each day during the summer period (1 June to 31 August) to best reproduce the observed phytoplankton dynamics. Assuming that all available SRP is utilized for primary production on a daily basis, this is equivalent to a sediment flux rate of 6.7 mg SRP m^{-2} d^{-1} and comparable to that reported earlier for Lake Engelsholm and other shallow Danish lakes (Jensen et al., 1992). PCLake includes a simple, but dynamic sediment nutrient pool, in which the release of nutrients from the sediments is related dynamically to the biogeochemical dynamics of the water column. For PCLake, calibration of phytoplankton dynamics was done mainly by modifications of internal nutrient storage parameters, maximum potential growth rates and zooplankton grazing parameters.

2.4. Future scenarios

Based on the EU ENSEMBLES project (van der Linden and Mitchell, 2009), where 19 regional climate models were used to generate an ensemble simulation of the Intergovernmental Panel on Climate Change (IPCC) A1B scenario for the location of seven major cities in Denmark (Boberg, 2010), three individual climate scenarios were derived (Table 1). Due to the uncertainty of the regional climate models, as well as the relatively small regional differences in projected future climate for the seven Danish locations, we used the average future climate derived from the seven locations (Boberg, 2010). In addition, two future nutrient load scenarios were generated and combined with the climate scenarios. Nutrient scenarios were generated by applying the same multiplication factor to all forms of nutrient species in the inflows (this factor would

then vary to generate scenarios with different percentages of change in external nutrient load). The nutrient scenarios were based on previous studies on the potential effects of future climate on total nitrogen (Jeppesen et al., 2011) and total phosphorus (Jeppesen et al., 2009) losses from land to waterways in Denmark.

The future climate scenarios were implemented by a simple delta-change method relative to daily air temperatures (using the same delta-change for each day throughout the years/seasons) of the base scenario (represented by years 1999-2001), where Scenario 1 represents climate of the year 2050, Scenario 2 represents climate of 2100, and Scenario 3 represents climate of 2100 for a more extreme warming of climate. All scenarios have previously been identified as plausible in the ENSEMBLES project (van der Linden and Mitchell, 2009), where these future scenarios were derived from probability density plots of projections by 19 individual regional climate models (Boberg, 2010). Results from the ENSEMBLES project suggest that precipitation by 2050 and 2100 will change, albeit to a small degree, generally with increases during winter and decreases during summer (of the order of $0.1 - 0.5$ mm day^{-1}) (Boberg, 2010). Assuming that no interventions take place in terms of land-use management, this may to some extent result in increased nutrient loads to lakes. Hence, total phosphorus and nitrogen loads to temperate Danish waterways may increase by roughly 5-15% by the year 2100 (Jeppesen et al., 2009; 2011). To reflect this case, we adopted two scenarios, both of which used the temperature increase of 5 ℃ as simulated in Scenario 3, but with phosphorus and nitrogen loads simultaneously increased by 5 % (Scenario 4) and 15 % (Scenario 5) (Table 1). To be able to evaluate the importance of increased nutrient loads relative to increased temperatures, an additional two scenarios were run, reflecting a 5 % and 15 % nutrient load increase, respectively, without any changes to temperatures (i.e. using baseline temperatures).

3. Results

3.1. Performance of the individual aquatic ecosystem models and the ensemble mean simulation

The three individual models generally performed to a similar level achieved in other peer-reviewed studies in terms of the r^2 and relative absolute error (RE) values between model simulations and observations of chlorophyll *a* (e.g., review by Arhonditsis and Brett, 2004, where median r^2 was 0.48 and RE was 44% for simulation of phytoplankton biomass across 153 individual modelling studies). The variation explained (r^2) by the models increased considerably by use of monthly means (Table 2), relative to day-by-day comparisons, and even further when excluding the single, extremely high chlorophyll *a* concentration recorded in September 2001. There were considerable differences between the simulations by the three models. While PCLake and PROTECH generally exhibited considerably higher r^2 values than DYRESM-CAEDYM for the calibration and validation periods, the three models showed similar performance in terms of the relative errors, and DYRESM-CAEDYM was generally best at reproducing the averages and median chlorophyll *a* levels for the entire three-year period 1999-2001 (Table 3). In general, the ensemble mean of all three models was superior to any of the individual models (Fig. 1) in describing total phytoplankton biomass for the whole 1999-2001 period (Table 2). Given the different model performance measures used, i.e. including day-by-day match and monthly means and all time periods used (listed in Table 2), we can take count of the frequency at which the individual models and the ensemble mean were superior for each of the 16 model performance measures. Here, by assuming that differences in model performance are negligible when r^2 values differ by 0.01 or less and RE values by 5 % or less, the ensemble mean was also superior, being the best or equal to the best in eight counts out of 16.

3.2. Future scenario projections by the ensemble mean simulation

Throughout the simulations of the three climate warming scenarios, where temperatures increase from SC1 through SC3, PCLake and DYRESM-CAEDYM suggest a considerable increase in

phytoplankton biomass relative to baseline. PROTECH also suggests a progressive increase in phytoplankton biomass with warming in the future scenarios, albeit the biomass in all the future scenarios was generally at levels slightly below the baseline (Table 4). The ensemble mean simulation suggested that total phytoplankton biomass will increase, in particular during summer months (Table 5), albeit that there are considerable variations between the individual model projections (Fig. 2). Concurrently, the contribution of cyanobacteria to the total phytoplankton biomass increased. The World Health Organization (WHO) suggests limits for cyanobacteria biomass for recreational water use of 10 and 50 mg m^{-3}, corresponding to, respectively, low and high probability that a short-term human exposure may cause skin irritations and gastro-intestinal illness (Chorus and Bartram, 1999). The number of days increased when biomass exceeded the WHO limits of 10 and 50 mg m^{-3} from 150 to 181 and 8 to 42 days per year, respectively.

When the very warm climate scenario (SC3) was combined with increased nutrient loads to generate scenarios SC4 and SC5, there was only a small effect observed in the ensemble mean simulations (Table 5, Fig. 2) relative to the effect of warming alone. Furthermore, when nutrient loads were increased by as little as 15 % (Fig. 2, SC5), there was even a tendency for the total phytoplankton biomass to decrease slightly, relative to the scenario where only temperatures were increased (SC3; Fig. 2). However, the modelled uncertainty for scenarios 4 and 5 was somewhat greater, as illustrated by a widening in the ensemble uncertainty range, suggesting that the three individual models were most divergent in their projections for these particular scenarios.

The effects of warming in scenarios SC1-SC3 were most pronounced for cyanobacteria biomass, with a considerable increase during summer (Fig. 3). Hence, whilst annual and summer total chlorophyll *a* in SC3 relative to the Base scenario increased on average by 18 and 48 %,

respectively, chlorophyll *a* contributed by cyanobacteria increased by 29 and 66 %, respectively. The combined effects of warming and increased nutrient loads showed little effect on cyanobacteria relative to warming alone. As was observed for total phytoplankton biomass, the ensemble mean simulation also suggested that cyanobacteria biomass could be slightly reduced in SC4 and SC5 relative to SC3, albeit that the model uncertainty was also greater for SC4 and SC5.

The importance of nutrient load increases (SC6 and SC7) relative to increased temperatures were generally minor, and hence the effects of the mild warming scenario (SC1) on both total phytoplankton and cyanobacteria biomass was greater than the effects of increasing nutrients loads by 15 % (Table 5).

4. Discussion

4.1. Perspectives of the ensemble modelling approach

Our study is the first to apply several individual complex dynamic lake models to the same aquatic ecosystem. The ensemble modelling approach has been used for a number of years for weather forecasts and global circulation models (GCMs), and is common practise when, for example, the IPCC reports on the potential effects of anthropogenic activities on future climate. An ensemble modelling approach can be applied either as a single-model ensemble, where multiple parameter combinations or multiple sets of initial conditions are run through a single model to produce variations (and derive a mean value) of output; or as a multi-model ensemble (as in present study), where multiple, different models are used, also providing variations in output. We found that the ensemble mean of the three models was superior to any of the individual models in describing the observed seasonal phytoplankton dynamics, which is in general agreement with the experiences

found in climate modelling studies (Palmer et al., 2005). From a climate modelling perspective, Tebaldi and Knutti (2007) elaborate that "for a single given diagnostic or variable, the multi-model performance might not be significantly better than the single best model, but studies indicate that the improvements are more dramatic if an aggregated performance measure over many diagnostics is considered", and Hagedorn et al. (2005) argue that the largest benefit is seen in "the consistently better performance of the multi-model when considering all aspects of the predictions". The meteorological and climate modelling communities have over a number of years built up a strong history for observation – and model-data sharing – hence facilitating ensemble modelling. This can to a large degree be explained by the fact the national meteorological institutes are all members of the World Meteorological Organization (WMO) and data exchanges are built into the organization charter. The same is not the case for lake-modelling. Sharing of observations and model results is currently done on a bi-lateral basis through direct/individual contact. Providing an open forum for exchange of observations, numerical models, model configurations and model results is of prime interest to the entire lake-modelling community and is necessary to adequately convey uncertainties in model projections to the wider community. Initiatives like the Global Lake Ecological Observatory Network (GLEON), where high-frequency data on water physics and selected chemical and biological attributes, collected from on-site monitoring buoys, are shared worldwide, could very well be followed and expanded to include exchange of additional data required to derive inputs to aquatic ecosystem models. With increased availability of collaborative tools via the internet the task is possible but will require a directed effort from individuals. Recent developments within the aquatic open source modelling community indicate both the need and potential for such studies to achieve this collaborative goal (Trolle et al., 2012).

4.2. Deriving uncertainty from the ensemble simulation

By applying three different models to the same lake, we were for the first time able to compare the uncertainty of simulated phytoplankton biomass (i.e. uncertainty due to different model structures). Hence, the uncertainty of the model projections, represented by the grey-shaded range delineated in the figures (e.g. Fig. 1), suggests that the uncertainty is greatest around the time when biomass peaks during spring and summer months. Therefore, the models generally tend to agree on the timing of a low-biomass phase, corresponding to a clear-water phase between the spring and summer blooms, as the uncertainty band clearly narrows around the ensemble mean (e.g. Fig. 1). For the scenarios, the uncertainty around the ensemble mean was largest for those scenarios where climate warming and increased external nutrient loads were combined, relative to the scenarios with warming alone. This can be explained by the different models' conceptual handling of nutrient cycling (e.g., Mooij et al., 2010), and how this cycle interacts with phytoplankton dynamics, as well as several other differences in the conceptual ecosystem models (e.g., cyanobacterial nitrogen fixation). For example, the state variable cyanobacteria in PROTECH was set up to be able to fix nitrogen, whereas in DYRESM-CAEDYM and PCLake it was not. Thus, when increasing nitrogen loads, the competitive advantage of cyanobacteria (during summers) relative to other phytoplankton types is somewhat reduced (in PROTECH), and consequently phytoplankton composition may change (potentially in favour of phytoplankton groups with smaller chlorophyll to biomass ratios), as seems to be the case particularly for the PROTECH simulations in our study (SC6 and SC7 in Table 4). This effect has been seen before in PROTECH studies (e.g., Elliott and May, 2008; Elliott, 2010). It has also been pointed out (Mooij et al., 2010) that improving the ability to describe interactions between nutrients in bottom sediments and the overlying water column is a key element for further enhancing model performance of aquatic ecosystem models. Such improvement would therefore also likely reduce the uncertainty of the models projections. There is little value in comparing nutrient dynamics and uncertainties between the three models, as nutrients are handled

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somewhat differently in each model, and occur as different species (e.g., DYRESM-CAEDYM operates with two species of organic detrital phosphorus, while PCLake operates with one, and PROTECH does not include organic phosphorus but rather uses inorganic phosphorus supply as a forcing function, which, for example, was used to calibrate an internal loading effect). The ensemble approach has helped identify this issue, and future model developments could fittingly include better alignment of state variables. Arhonditsis and Brett (2004) also showed that model performance generally declines as simulations transition from physical/chemical to biological components of planktonic systems. Our findings support this, as exemplified by DYRESM-CAEDYM simulations, where r^2 and RE values between modelled output and observations were 0.71 and 26.0 % for total nitrogen and 0.44 and 25.9 % for total phosphorus concentrations, respectively, relative to 0.01 and 121 % for total phytoplankton biomass for the period 1999-2001.

Based on our results, routes for future research emerge, including further identification and quantification of processes that are causing the greatest variability between models and a subsequent improvement of individual conceptual models to enhance model fit and reduce uncertainty. Ideally, such studies would involve multi-lake comparisons, thus enabling validation of model performance for systems with contrasting ecosystem behaviours (e.g., systems dominated by pelagic versus benthic primary production). One example of a relevant focal point, which was revealed during the calibration and validation process of the present study, is the rather dramatic oscillations in phytoplankton biomass simulated by DYRESM-CAEDYM in the summer periods. Such oscillations do not appear in observations, nor in PCLake and PROTECH during summer months, and consequently the r^2 values achieved for DYRESM-CAEDYM were generally low (as also seen in other applications of this model, e.g., Trolle et al., 2011; Özkundakci et al., 2011). In contrast to PCLake and PROTECH, DYRESM-CAEDYM includes detailed high-frequency

hydrodynamics, which can influence phytoplankton concentrations and vertical distributions in the short-term (sub-daily and daily), and thus generally cause greater output variability. An additional effect, and likely more important mechanism behind the output variations from DYRESM-CAEDYM, is the feedback mechanism between zooplankton and phytoplankton. In DYRESM-CAEDYM this feedback is dynamic (and similar to the traditional Lotka–Volterra predator–prey model) and not implicitly mediated by, for example, vegetation biomass as in PCLake, while the zooplankton dynamics in PROTECH are implemented by a simple mortality rate on phytoplankton. A relevant parallel to this is the history of the Ecopath/Ecosim model (focussing on trophic interactions of fish), which was traditionally based on Lotka–Volterra predator–prey type interactions. However, by developing the foraging arena theory (in which only part of the prey is available for predation; Walters and Christensen 2007), the developers of Ecopath/Ecosim were able to dampen the interactions between predators and prey (and reduce output variability in biomass for these state variables) and thereby achieve model outputs that more readily reproduced observations from the real world (while also improving the conceptual model). A similar development would therefore likely increase the predictive abilities of DYRESM-CAEDYM.

4.3. Future projections by the ensemble simulations

Long-term effects of climate change (e.g. by the year 2100) have previously been studied using models (e.g., Elliott et al., 2005; Mooij et al., 2007; Trolle et al., 2011) with conclusions similar to ours, that overall phytoplankton biomass is likely to increase, and cyanobacteria will become a more dominant feature of the phytoplankton species composition. In the model simulations, the effects on cyanobacteria are included both directly through influence of temperature on growth rate, and indirectly, e.g., through changes in water column stability and changes in nutrient transformation rates. The increase in dominance of cyanobacteria with warming also concurs with

empirical observations from time-series (Jöhnk et al., 2008; Posch et al., 2012) and cross-system analyses (Jeppesen et al., 2009; Carey et al., 2012; Kosten et al., 2012). However, the effects may be even more pronounced than projected by our model exercise, as the models cannot fully account for structural changes in the lake ecosystems that could occur due to warming. Hence, recent cross latitude studies indicate that, as a consequence of warming, the composition of fish stocks can be expected to change towards higher dominance of zooplanktivorous and omnivorous fish, and towards smaller and faster reproducing fish, implying increased predation on zooplankton and, consequently, less grazing on phytoplankton (i.e., less top-down control), and a higher chlorophyll:TP ratio (higher yield) (Jeppesen et al., 2010a;b; Meerhoff et al., 2012). In addition, the alleviating effects of aquatic plants on water clarity seem weaker in subtropical lakes than in north temperate lakes (Jeppesen et al., 2007). These findings all point to even higher algal biomass and higher proportion of cyanobacteria, due to changing structural aspects of warming lakes, than can be projected by the current models. An important aspect for further improving the reliability of model projections is to be able to test/validate the models against observation data. As we have no data truly reflecting future conditions, a key challenge is therefore to rigorously test models using proxies of future conditions (Refsgaard et al., 2013). Ideally, one would be able to perform differential-split sample tests, using periods with apparent different climatic conditions (e.g., dry/wet or cold/warm) where calibration is performed on one period and validation on another period (Refsgaard et al., 2013). This was not possible in our study where, for example, annual average whole-water column temperature varied less than 0.5 °C between the three years available for calibration and validation.

In our study, despite the relatively modest increases in air temperature of the 2050 near-future scenario (+1.5 $^\circ$C, SC1), the ensemble simulation suggests that the number of days when the

cyanobacteria biomass exceeds the highest WHO limit will increase considerably, from 8 to 23 days per year. Lake Engelsholm has an intensively managed, temperate catchment, and is typical of many lowland lake ecosystems in terms of area (out of 120,000 Danish lakes, more than 95% has a surface area < 1 km^2), trophic status and species composition. It is therefore very likely that many other lakes could follow a similar trajectory that may be interpreted as a degradation of the lake ecosystem.

Given that, the implications of these results are potentially even more important because scenarios SC1-SC3 show a deterioration in ecological quality through increased cyanobacteria biomass even when the nutrient supply to the lake was kept at its present day levels. Therefore, if lake managers do nothing to change a lake's trophic status, the lake's ecological quality could still become worse, producing a new threat to freshwaters independent of eutrophication. This logic can be further extended to suggest that lakes which currently do not have a problem with cyanobacterial blooms because they are less nutrient rich, could through climate change experience new problems. This effect would increase the number of lakes which fail ecological quality criteria such as stipulated by the European Union Water Framework Directive without changes in their trophic status. Therefore, the potential of climate change to alter the traditional relationship between nutrient status and chlorophyll (Vollenweider and Kerekes, 1980) is abundantly clear from the results of this study.

5. Conclusions

We examined the performance of multiple aquatic ecosystem models in terms of their ability to reproduce phytoplankton biomass in a typical lowland temperate lake. The suite of models was subsequently used to project the effects of climate warming on phytoplankton biomass, and thus the potential future implications for water users. We found that; 1) using the mean of all models

generally was superior to any individual model in reproducing observed phytoplankton dynamics; 2) in a typical lowland temperate lake, future climate warming may cause the average number of days per year when cyanobacteria biomass exceeds World Health Organization recommended limits to increase, from 8 to 23 days per year, with only modest increases in air temperature; 3) climate warming will facilitate higher yields of both cyanobacteria and total phytoplankton biomass relative to nutrient supply; 4) future climate change imposes a serious threat to the quality freshwater resources.

6. Acknowledgements

7. References

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Tables

Table 1. Potential future climate and nutrient load scenarios relative to base scenario (years 1999-2001). Climate projections are based on the ENSEMBLES project (van der Linden and Mitchell, 2009; Boberg, 2010).

	Scenario details	Daily temperature change relative to base (ºC)	Increase in total nitrogen and phosphorus loads relative to base (%)
Scenario 1	Indicative of warming by year 2050	1.5	0
Scenario 2	Indicative of warming by year 2100	3	0
Scenario 3	Indicative of high warming by year 2100	5	0
Scenario 4	Indicative of high warming and increased precipitation by year 2100	5	+5
Scenario 5	Indicative of high warming and highly increased precipitation by year 2100	5	+15
Scenario 6	Nutrient loading increase by 5%	0	+5
Scenario 7	Nutrient loading increase by 15%	0	+15

Table 2. Summary of calibration (1999-2000) and validation (2001) statistics pertaining to total chlorophyll *a* for individual models and for the ensemble mean of all models.

		R^2				RE			
		1999-2000	2001	2001*	1999-2001	1999-2000	2001	2001*	1999-2001
Day-by-day match	PCLake	0.34	0.24	0.33	0.24	121	120	123	121
	DYCD	0.01	0.01	0.02	0.01	102	162	167	121
	PROTECH	0.49	0.05	0.31	0.24	72	102	103	82
	Ensemble mean	0.47	0.13	0.32	0.27	83	113	115	92
Monthly means	PCLake	0.48	0.68	0.62	0.44	65	74	77	67
	DYCD	0.13	0.04	0.27	0.08	59	103	106	73
	PROTECH	0.55	0.11	0.31	0.31	53	101	103	68
	Ensemble mean	0.61	0.36	0.53	0.45	39	79	80	52

* Excluding the September 2001 observation of 150 mg Chl *a* m^{-3}

Table 3. Annual and summer averages and medians of observed and simulated total chlorophyll *a* for the three year period 1999-2001.

		Total chlorophyll *a* (mg m^{-3})		Deviation from observed (%)	
		Annual	Summer	Annual	Summer
Observed	Average	26.5	28.1	-	-
	Median	21.8	24.0	-	-
PCLake	Average	24.5	27.4	-7.7	-2.7
	Median	16.9	20.5	-22.6	-14.5
DYCD	Average	24.5	25.2	-7.5	-10.2
	Median	23.2	22.7	6.5	-5.6
PROTECH	Average	14.4	16.5	-45.6	-41.5
	Median	10.8	12.0	-50.5	-50.0
Ensemble mean	Average	21.2	23.0	-20.3	-18.1
	Median	17.0	18.7	-22.1	-22.1

Table 4. Simulated annual and summer (June-August) averages in baseline and future scenarios for total chlorophyll *a* and cyanobacterial chlorophyll *a*.

	Total chlorophyll *a* (mg m^{-3})		Cyanobacteria (mg m^{-3})		Cyanobacteria contribution (%)	
	Annual	Summer	Annual	Summer	Annual	Summer
PCLake-base	24.5	46.6	15.6	25.2	63.8	54.1
PCLake-SC1	28.2	57.8	23.0	46.7	81.6	80.8
PCLake-SC2	31.0	68.9	27.8	63.7	89.7	92.4
PCLake-SC3	33.6	80.3	31.7	78.0	94.2	97.2
PCLake-SC4	33.9	80.8	31.9	78.5	94.1	97.1
PCLake-SC5	34.4	81.9	32.4	79.5	94.0	97.1
PCLake-SC6	24.6	46.5	15.8	25.7	64.1	55.4
PCLake-SC7	24.9	47.2	16.1	26.5	64.6	56.3
DYCD-base	24.5	28.4	11.0	24.2	44.8	85.1
DYCD-SC1	25.7	30.8	11.9	27.2	46.3	88.5
DYCD-SC2	25.6	31.7	13.2	28.7	51.5	90.6
DYCD-SC3	27.0	36.2	15.0	33.4	55.6	92.2
DYCD-SC4	27.2	36.4	15.0	33.5	55.1	91.9
DYCD-SC5	28.8	37.5	15.0	34.3	51.9	91.4
DYCD-SC6	23.9	28.5	11.1	24.2	46.2	84.9
DYCD-SC7	24.2	27.4	11.2	23.1	46.4	84.3
PROTECH-base	14.4	32.3	10.9	24.2	75.7	74.8
PROTECH-SC1	12.6	27.4	8.5	18.2	67.5	66.3
PROTECH-SC2	12.7	28.1	8.7	19.2	68.5	68.2
PROTECH-SC3	13.8	31.7	9.9	23.7	72.2	74.8
PROTECH-SC4	13.8	30.9	9.8	22.3	70.6	72.1
PROTECH-SC5	10.4	19.0	5.9	9.6	56.4	50.3
PROTECH-SC6	12.0	26.3	8.2	17.8	68.2	67.8
PROTECH-SC7	11.1	22.9	7.1	14.2	64.3	61.8

Table 5. Summary of ensemble mean results from the scenario simulations based on annual and summer (June-August) averages.

| | Total chlorophyll *a* (mg m^{-3}) | | % cyanobacteria biomass of total chlorophyll *a* | | Days per year exceeding WHO limits (cyanobacterial chlorophyll *a*) | |
	Annual	Summer	Annual	Summer	Limit: 10 mg m^{-3}	Limit: 50 mg m^{-3}
Base	21.1	28.9	59.2	51.7	150	8
SC1	22.2	30.2	65.3	66.0	157	23
SC2	23.1	34.1	71.7	77.7	172	27
SC3	24.8	42.8	76.1	85.9	181	42
SC4	25.0	41.8	75.6	84.9	180	37
SC5	24.5	40.0	72.2	84.3	175	27
SC6	20.2	29.0	57.8	52.9	149	5
SC7	20.1	28.5	57.2	52.5	160	0

Figure captions

Figure 1. Calibration and validation of the three ecosystem models relative to the ensemble mean simulation. Calibration (1999-2000) and validation (2001) of the three ecosystem models (line plots) to observed phytoplankton dynamics (red circles in scatter plot). The blue shaded "Band" represents the total range (maximum/minimum) of the three models and the thick black "Mean" line represents the ensemble mean of all three models. PCLake is represented by purple line, DYRESM-CAEDYM (DYCD) by blue line and PROTECH by green line.

Figure 2. The responses of simulated total phytoplankton biomass to climate change scenarios. The ensemble mean simulation of total phytoplankton biomass (chlorophyll *a*) for scenarios (SC) 1-7 (red lines) relative to the uncertainty range of the three models (blue shaded band), and the ensemble mean from the base simulation (black line).
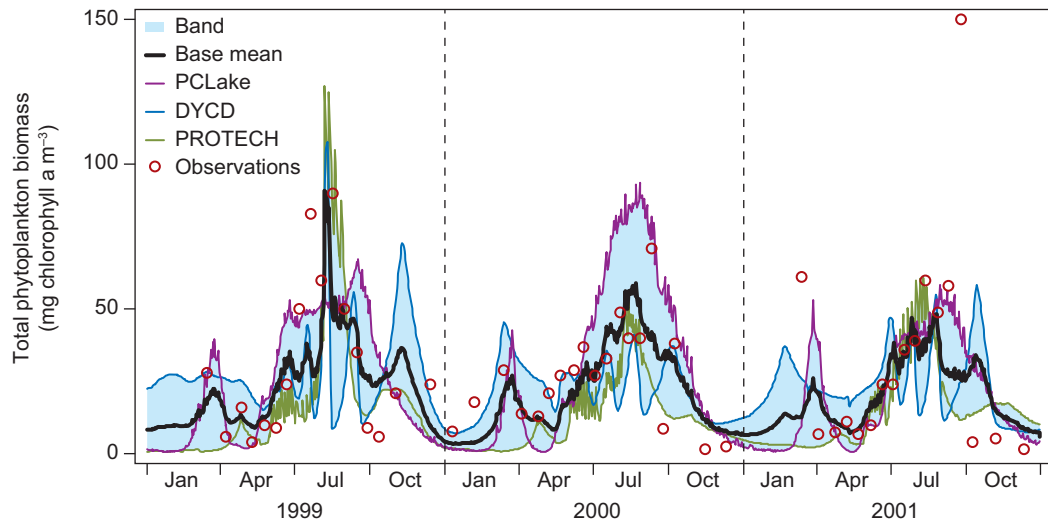
Figure 3. The responses of simulated cyanobacteria biomass to climate change scenarios. The ensemble mean simulation of cyanobacteria biomass (chlorophyll *a*) for scenarios 1-7 (red lines) relative to the uncertainty range of the three models (blue shaded band), and the ensemble mean from the base simulation (black line).
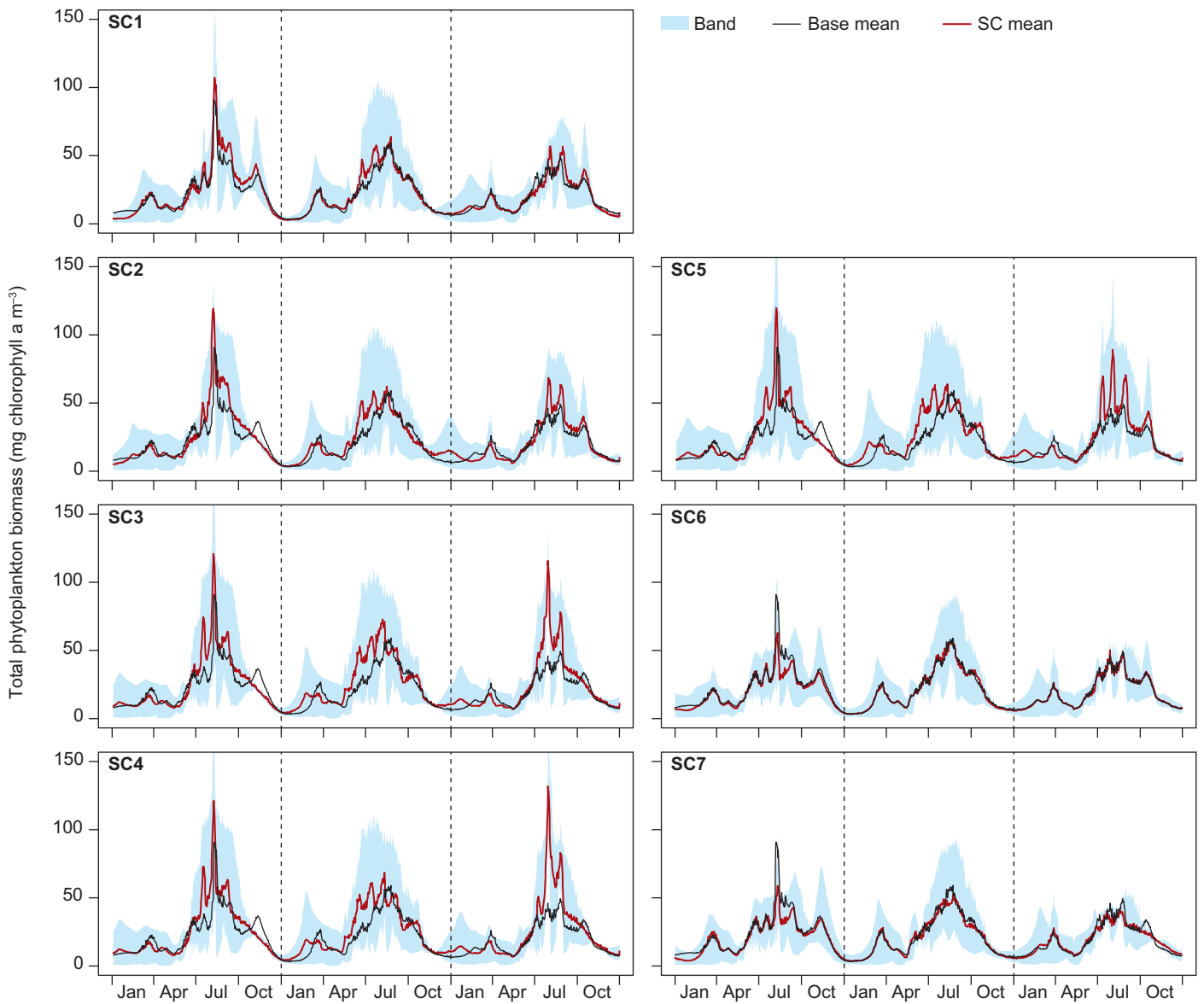
Fig. 1.

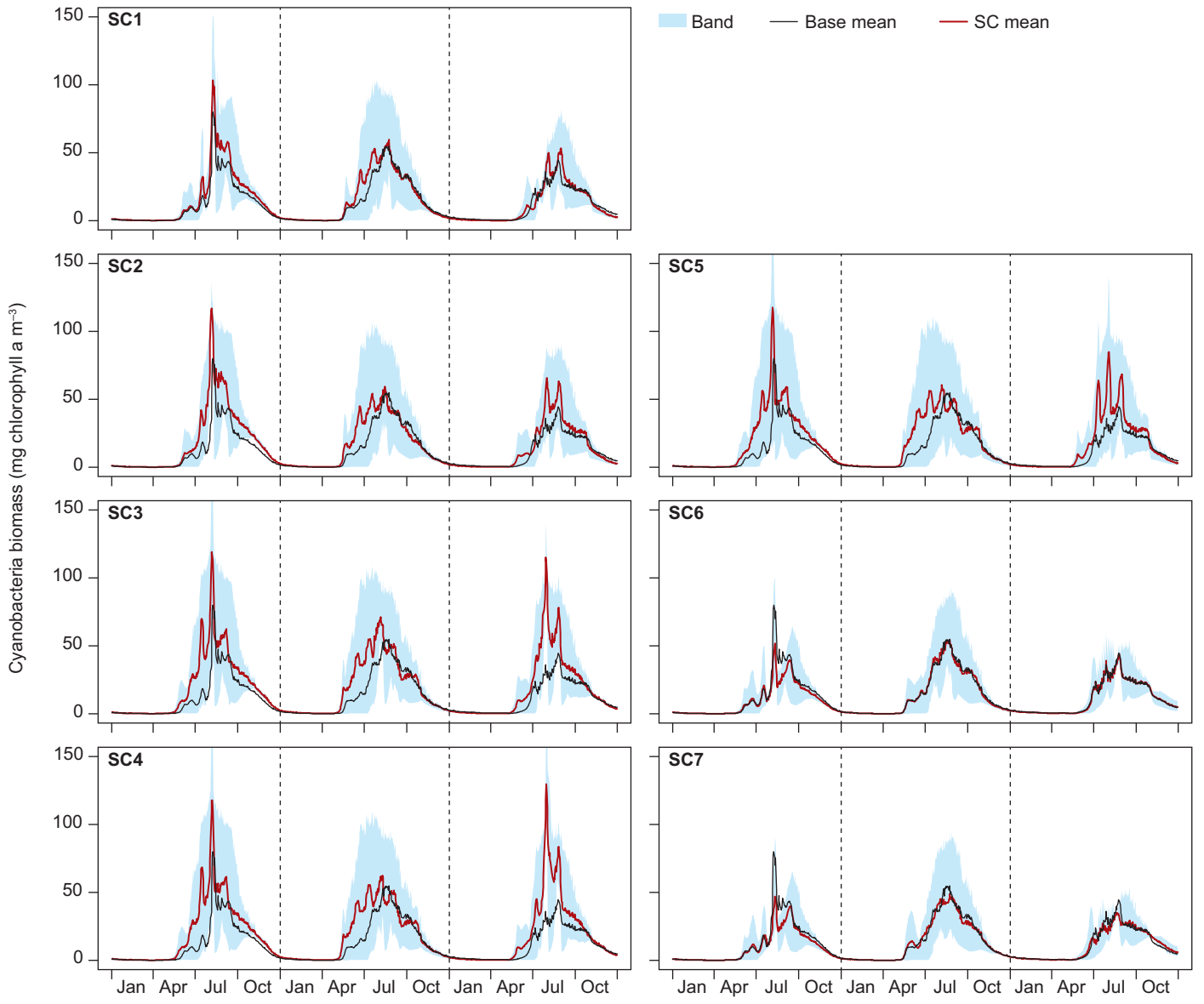
Fig. 2.

Fig. 3.