

## Reconciling observed and modelled phytoplankton dynamics in a major lowland UK river, the Thames

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### ABSTRACT

This study aims to elucidate the key mechanisms controlling phytoplankton growth and decay within the Thames basin through the application of a modified version of an established river-algal model and comparison with observed stream water chlorophyll-*a* concentrations. The River Thames showed a distinct simulated phytoplankton seasonality and behaviour having high spring, moderate summer and low autumn chlorophyll-*a* concentrations. Three main sections were identified along the River Thames with different phytoplankton abundance and seasonality: (i) low chlorophyll-*a* concentrations from source to Newbridge; (ii) steep concentration increase between Newbridge and Sutton; and (iii) high concentrations with a moderate increase in concentration from Sutton to the end of the study area (Maidenhead). However, local hydrologic (e.g. locks) and other conditions (e.g. radiation, water depth, grazer dynamics, etc.) affected the simulated growth and losses. The model achieved good simulation results during both calibration and testing through a range of hydrological and nutrient conditions. Simulated phytoplankton growth was controlled predominantly by residence time, but during medium–low flow periods available light, water temperature and herbivorous grazing defined algal community development. These results challenge the perceived importance of in-stream nutrient concentrations as the perceived primary control on phytoplankton growth and death.

**Key words** | algae, dynamic model, environmental controls, phytoplankton, River Thames, seasonality

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### INTRODUCTION

Phytoplankton is essential for life as being the base of the aquatic food chain (Reynolds 1984) and, in some cases, improving the water quality of large rivers by removing nutrients and providing oxygen during low-flow periods (Wehr & Descy 1998; Picard & Lair 2005). Phytoplankton can also become a nuisance, especially in rivers and lakes, when present in large numbers. The presence of phytoplankton in drinking water can affect the colour, taste and odour of water, can clog pipes and causes filtration problems (Jones 1984). The removal of excessive algae can increase the cost of water treatment (Steffensen 2008). The overabundant presence of phytoplankton also negatively affects the recreational use of water bodies; toxic species can affect the fish population (i.e. poison fish tissues with toxins) and can also cause

skin irritation and stomach problems in humans (Wehr & Descy 1998).

Extensive studies of lakes uncovered the underlying key factors of eutrophication in standing waters (Marcus 1959), but the understanding of eutrophication of rivers is much more limited (Hilton *et al.* 2006). The linkages between environmental factors and phytoplankton growth are sufficiently known to identify the important processes and create numerical models (Reynolds *et al.* 2001). These models, which simulate the effect of hydrological, chemical and meteorological conditions on ecology, facilitate the understanding of the integration of hydrological conditions and biogeochemical processes and their relationship with in-stream ecology. Such models help the exploration of the management options. Attempts have been reported in the

literature to create dynamic models to simulate phytoplankton in lakes and rivers with different complexities. Simple models (Whitehead & Hornberger 1984; Cloot & Le Roux 1997; Thebault & Qotbi 1999; Sellers & Bukaveckas 2003; Guven & Howard 2006; Chapra *et al.* 2007) focus on only one or a few environmental variables (light, nutrients, temperature) whereas complex models consider factors and processes in much greater detail, often at species level (Kowe *et al.* 1998; Griffin *et al.* 2001; Reynolds *et al.* 2001; Park *et al.* 2008). This complexity often limits their applicability due to the high parameter and data demands (Sourisseau *et al.* 2008).

The aim of this research was to create a medium complexity phytoplankton model that considered the main environmental factors and processes with a balanced trade-off between data requirement, model complexity and useful output, and to use the model to help understand the observed patterns in stream water chlorophyll-*a* concentration data. This new phytoplankton model used the existing algae model of Whitehead & Hornberger (1984) as a basis, which simulated the growth of both live and dead organic matter in the water column and their downstream transport. Many scientific papers recognised the importance of water column nutrients (e.g. Jeppesen *et al.* 2000; Neal *et al.* 2006), water temperature (e.g. Lack 1971; Levasseur *et al.* 1984; Coles & Jones 2000) and grazing (e.g. Walton *et al.* 1995; Kobayashi *et al.* 1996; Gosselain *et al.* 1998; Griffin *et al.* 2001), which were not included in the Whitehead & Hornberger (1984) model. Modifications were therefore made to the original model structure and equations are proposed here to account for these factors.

Previous field-based research found that phytoplankton growth in the River Thames was limited neither by flow nor phosphorus, and that the growth period is normally between March and August with a peak in the April–May period (Lack 1971; Young *et al.* 1999). It was also found that the water of the River Thames is well mixed, and thus phytoplankton populations can be estimated by using the observation at the water surface (Kowalczewski & Lack 1971). Neal *et al.* (2006, 2010a, b, c) observed a lack of response in chlorophyll-*a* levels to reduced soluble reactive phosphorus (SRP) levels in sewage treatment plant effluents, which indicated that the observed nutrient levels were still too high to control algal growth in the River Thames. In the same study, a strong

linear correlation between residence time and chlorophyll-*a* and the spring–summer chlorophyll-*a* levels also positively correlated with SRP, particulate nitrogen, particulate organic carbon and suspended sediments.

The River Thames was previously modelled by Whitehead & Hornberger (1984), but the general phytoplankton behaviour was not discussed in their paper. The phytoplankton in the River Thames was also simulated by the PROTECH-C model (Reynolds *et al.* 1998) but, until now, the report and the results are not available in the public domain. This modelling paper therefore provides useful insights to phytoplankton behaviour in the Thames catchment.

This paper describes the key factors and processes that control river-system phytoplankton dynamics in a major UK river system, the River Thames, based on a model-based assessment and water quality gathered within an operational network by the Environment Agency and the Centre for Ecology and Hydrology (CEH). As such, the work builds on and complements other model-based assessments through the development and application of a modified version of the river-algal model developed by Whitehead & Hornberger (1984). Such models are needed to aid environmental management by helping to optimise the flow and pollution mitigation measures and restoration options set against a background of population growth and climate change (Johnson *et al.* 1998; Pretty *et al.* 2002; Kinniburgh & Barnett 2010). In particular, the development of dynamic process-based models for application in river (rather than lake) systems is a topic requiring exploration (Hilton *et al.* 2006). The River Thames is a major UK river basin that has been monitored extensively and water quality is expected to be under severe pressure in the coming decades; population growth has resulted in increasing sewage effluent inputs and more intense farming practices. There is therefore a pressing need to understand the condition of eutrophication in this system and assess the potential management options to improve the ecological status. This paper briefly describes the applied model and presents the River Thames (UK) application of this model.

## STUDY AREAS AND DATA RESOURCE

The Thames Basin is the major catchment in southeast England (area 16,133 km<sup>2</sup>, length 344 km). This study

focuses on the upper and middle reaches from the source to Maidenhead (187 km river length), where tidal movement and salinity do not affect the hydrology and water quality of the river (Figure 1). The main tributaries of the study area include the River Cherwell, River Thame and River Kennet. The source area of the Thames is characterised by Jurassic limestone (Sommerford), but the bedrock changes to a mixed gravel-sand-clay deposit near Oxford. The lower sections of the study area (around Reading) have a Cretaceous chalk geology. The mean annual flow changes substantially downstream, being  $1 \text{ m}^3 \text{ s}^{-1}$  at Cricklade (BFI: 0.67),  $15 \text{ m}^3 \text{ s}^{-1}$  at Farmoor (BFI: 0.65);  $27 \text{ m}^3 \text{ s}^{-1}$  at Sutton (BFI: 0.64),  $37 \text{ m}^3 \text{ s}^{-1}$  at Reading (BFI: 0.66) and  $58 \text{ m}^3 \text{ s}^{-1}$  at Bray Weir (BFI: 0.70), which is downstream of Maidenhead.

The Base Flow Index (BFI) measures the proportion of river discharge that originates from stored sources and is an indication of catchment geology. The flow is moderately groundwater dominated in the upper and middle sections of the River Thames. The mean total precipitation is between 700 and 800 mm per year, which is relatively dry when compared to the UK average ( $800\text{--}1,300 \text{ mm a}^{-1}$ ). The catchment is predominantly rural upstream of Reading, becoming more urban further downstream. Nonetheless, there are urban and peri-urban effluent inputs from towns

such as Swindon, Banbury and Oxford. The main Sewage Treatment Works (STWs) discharging directly into the Thames are Swindon STW (Population Equivalent or PE 157,000), Cassington STW (PE 14,000), Abingdon STW (PE 12,432), Goring STW (PE 7,180) and Cricklade STW (PE 4,070). The flow in the Thames is heavily modified by the 36 locks and weirs between Farmoor and Teddington in order to maintain navigation and flows. The locks reduce the flow velocities and increase the travel time. This allows the phytoplankton population to grow and potentially reach nuisance levels.

## METHODOLOGY

The conceptual diagram of the applied in-stream algae model is shown in Figure 2. The model simulates the live suspended algae (SA), the dead entrained organic matter (EOM) and the biomass of herbivorous grazers. SA species are not differentiated, and the total phytoplankton is modelled. Both the SA and the EOM are free-floating; they are therefore subject to longitudinal transport with the river flow. Within the model, SA are also the subject of growth, death, settling and grazing, whereas the EOM is affected by the processes of sedimentation and bed-sediment

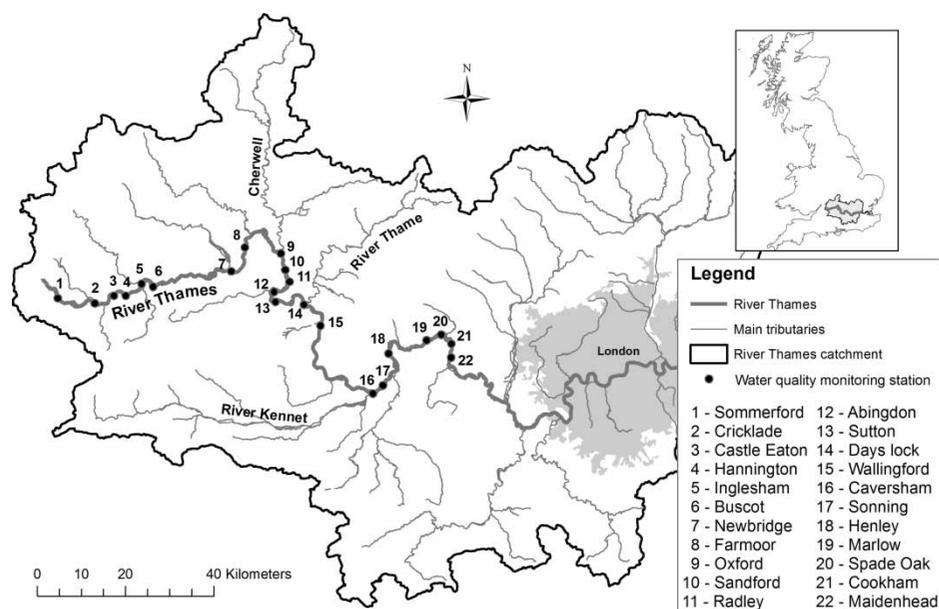
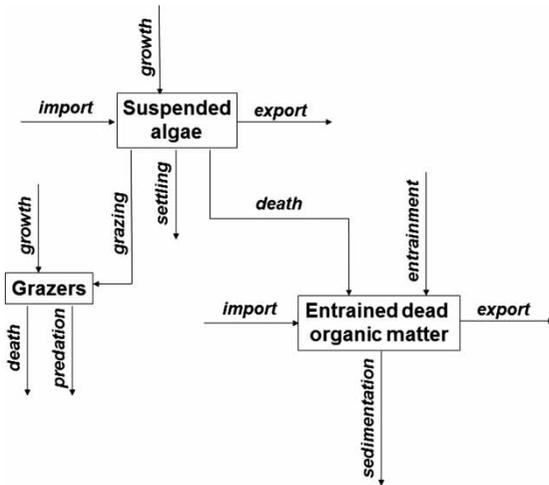


Figure 1 | The River Thames study area and monitoring station locations.



**Figure 2** | Conceptual diagram of the algae stream model.

enainment. The biomass of grazers is affected by their own growth and predatory and non-predatory mortality.

The algal model simulates at a daily time step and calculates reach average concentrations: each reach represents a continuously stirred tank reactor (CSTR). The reaches are chained to route the water from source to Maidenhead providing the longitudinal transport pathway of water, pollutants and biota. The CSTR concept is widely used in modelling studies (e.g. Whitehead *et al.* 1998; Guven & Howard 2006). This phytoplankton model requires four daily time series for each reach: inflow discharge into the reach, SRP concentration in the reach, water or air temperature and solar radiation.

The in-stream hydrology is modelled by a simple approach used in the integrated catchments (INCA) models (e.g. Whitehead *et al.* 1998). The ecological (phytoplankton) part of the model works on a ‘gram carbon’ unit basis ( $\text{g C day}^{-1}$ ). The change in water column chlorophyll-*a* ( $m_{\text{SA}}$  and  $m_{\text{EOM}}$  in units of  $\text{g C day}^{-1}$ ) is described with two mass-balance equations:

$$\frac{dm_{\text{SA}}}{dt} = \text{import}_{\text{SA}} + \text{growth}_{\text{SA}} - \text{death}_{\text{SA}} - \text{settling}_{\text{SA}} - \text{grazing}_{\text{SA}} - \text{export}_{\text{SA}} \quad (1)$$

$$\frac{dm_{\text{EOM}}}{dt} = \text{import}_{\text{EOM}} + \text{death}_{\text{SA}} + \text{enainment} - \text{sedimentation}_{\text{EOM}} - \text{export}_{\text{EOM}} \quad (2)$$

The mathematical expressions for the terms in Equations (1) and (2) are listed in Table A.1 in the appendix together with the list of model parameters (Table A.2) (Appendix available online at: <http://www.iwaponline.com/nh/043/028.pdf>). The key assumptions are as follows.

- There is evidence that the biomass:chlorophyll-*a* ratio of algae changes with increasing grazing (Walton *et al.* 1995); specifically, the algal community shifts to more filamentous upon severe grazing, regardless of enrichment. To simplify the model, this ratio was assumed to be constant in this model ( $\text{Ratio}_{\text{C:Chla}}$ ).
- To accommodate the dominance of different algal groups in the simulation, the model allows the selection of up to three optimum solar radiations ( $R_{\text{opt}}$ ) and three optimum temperatures ( $T_{\text{opt}}$ ) for phytoplankton. However, only one solar radiation and one temperature-related shape parameter can be selected ( $R_{\text{exp}}$ ,  $T_{\text{sh}}$ ), which will be used for all simulated algal groups. The model solves the radiation and temperature limitation equations for each algal group, and uses the least limiting value in the growth calculation (rows 5–6 in Table A.1).
- Phytoplankton is mostly grazed by zooplankton. Predation on zooplankton is considered with the presence of fish. Young fish hatch during spring and summer and they eat most zooplankton in late summer and autumn, when the water temperature is also expected to be at the maximum. The use of the Arrhenius temperature limitation formula (row 14 in Table A.1) therefore approximately represents the change in the biomass of predators throughout the year (Broughton & Jones 1978).
- The model is forced to keep a minimum biomass for grazers in each reach to ensure the biomass increment if conditions are favourable for growth. Therefore, if the simulated biomass falls below the user-defined value ( $m_{\text{grazers,min}}$  in units of  $\text{g C m}^{-2}$ ), on the next day the starting biomass of grazers will be  $m_{\text{grazers,min}}$  again.
- Enainment of organic matter was found to be a key process in the River Kennet (one of the main tributaries of the River Thames) during the preliminary data assessment, which indicated that at least half of the chlorophyll peaks resulted from turbulent flow conditions and not from true phytoplankton blooms (Jarvie *et al.* 2003; Lázár 2010). The enainment of dead organic matter

was therefore also included in the model. The simulation of the entrainment of the organic matter (live and dead) is difficult in river systems because it depends on a number of factors including hydraulic characteristics of the reach, substrate type and growth pattern of fixed vegetation, which constantly vary both spatially and temporally. This model only considers the dead organic matter entrainment (row 15 in Table A.1) to eliminate the uncertainty of the assumptions on the growth and entrainment of live benthic algae.

- The model only calculates the advection of phytoplankton; diffusion is not considered because the water column is probably well mixed (Kowalczewski & Lack 1971).

## MODEL SET-UP AND CALIBRATION

The location of the flow gauging stations and water quality monitoring sites and a summary of available data is given in Figure 1 and Table A.3, respectively (see <http://www.iwaponline.com/nh/043/028.pdf> for the Table A.3). The study area was divided into 33 reaches based on the locations of STWs and water quality monitoring and gauging stations. Reach lengths and subcatchment areas were calculated from a Digital Elevation Model or DEM (10 m grid of height values) accessed through EDINA and derived from Ordnance Survey (OS) data and river network shape files supplied by the CEH. The average reach widths were estimated by using Carto Maps sourced from EDINA (1:10,000 OS mapping).

This modified algae model has no terrestrial hydrological component and the diffuse discharge entering the reaches was assumed to be proportional to the area of the subcatchments. This was calculated from the discharge time series of the nearest gauging stations (Environment Agency or EA).

In the case of the solar radiation and air temperature data, the nearest UK Meteorological Office (UKMO)-Midas stations (British Atmospheric Data Centre, BADC) were used to compile a radiation and air temperature time series for each reach. To fill the gaps in the water temperature observations, the input water temperature time series was calculated by considering both the Automated Water Quality Monitoring Stations' water temperature (AWQMS,

EA) and UKMO-Midas (BADC) near-surface air temperature data and by using the Mackey & Berrie (1991) equation (water temp =  $x + y \times$  air temperature). This equation was calibrated ( $x$  and  $y$  parameters) against the measured mean daily AWQMS water temperature data. The correlation coefficients of the water temperature calibrations ranged from 0.85 to 0.90 for the River Thames.

These applications used EA and CEH water quality data (SRP, suspended sediment, chlorophyll-*a*) with varying measurement frequencies. The proposed model works on a daily time step; the gaps between phosphorus and suspended sediment measurements were therefore filled with the value of the last observation.

The initial values of the model parameters were selected from the scientific literature (Table 1). These were modified during the calibration to achieve a better fit to the observations, but all parameter values were kept within the literature ranges.

The calibration and validation test periods were 1997–2000 and 2001–2003, respectively. Model goodness-of-fit was assessed using Pearson product moment correlation ( $R^2$ ) and Nash–Sutcliffe (NS) statistics.

## RESULTS

The simulated stream water chlorophyll-*a* concentrations followed the observed pattern well in almost all reaches of the Thames in the calibration period (Figure 3). This was reflected in the high  $R^2$  goodness-of-fit coefficients, especially for the lower reaches where  $R^2$  was 0.87 at Sutton and 0.60 at Cookham Bridge. However, positive NS coefficients in the calibration period were only achieved at Abingdon Weir (NS: 0.37; 111 observations), Sutton (NS: 0.70; 31 observations) and Cookham Bridge (NS: 0.31; 42 observations). The overall model performance was slightly better in the validation test runs ( $R^2$ : 0.00–0.98) than in the calibration period ( $R^2$ : 0.01–0.87). In the validation test, all the lowest reaches (from Caversham to Cookham Bridge) were simulated with positive NS coefficients (NS: 0.20–0.62). Based on the visual assessment of the test period results, the low concentration values were captured well by the model and the timing of the higher peaks was correct, but the magnitudes of these higher peaks were

**Table 1** | Parameter values used in the model application

Parameter name	ID	Unit	Literature values	River Thames
Suspended algae (SA)				
Maximum growth	$k_3$	day <sup>-1</sup>	0.1–5.65 <sup>a</sup> ; 1.0–2.7 <sup>b</sup> ; 0.28–11 <sup>h</sup>	1.66
Non-predatory mortality	$k_4$	day <sup>-1</sup>	0.096 <sup>a</sup> ; 0.003–0.17 <sup>b</sup>	0.096
Half-saturation for P	$k_5$	µg P l <sup>-1</sup>	2–25 <sup>a</sup> ; 0.5–80 <sup>b</sup> ; 2–1,520 <sup>h</sup>	10
Self-shading	$k_7$	µg Chl <i>a</i> l <sup>-1</sup>		130
Opt. temperature 1	$T_{opt}$	°C		10.5
Opt. temperature 2	$T_{opt}$	°C		15
Opt. temperature 3	$T_{opt}$	°C		21
Temp. shape factor	$T_{sh}$	∅	2.3 <sup>d</sup> ; 1.88 <sup>e</sup> ; 1.6 <sup>f</sup> ; 1.4 <sup>g</sup>	2.3
Opt. solar radiation 1	$R_{opt}$	kJ m <sup>-2</sup>		11,000
Opt. solar radiation 2	$R_{opt}$	kJ m <sup>-2</sup>		16,900
Opt. solar radiation 3	$R_{opt}$	kJ m <sup>-2</sup>		24,000
Opt. solar rad. exp. Term	$R_{exp}$	∅		1.7
Sedimentation rate	$k_{13}$	day <sup>-1</sup>	0.1–15 <sup>a</sup> ; 0.02–0.6 <sup>b</sup> ; 0.02–14.7 <sup>h</sup>	0.3
Entrained organic matter (EOM)				
Sedimentation rate	$k_{15}$	day <sup>-1</sup>	0.6 (small sediment) <sup>c</sup>	0.6
Entrainment coeff.	$k_{16}$	gC m <sup>-2</sup> m <sup>-3</sup>		10 <sup>-16</sup> –10 <sup>-11</sup>
Entrainment coeff.	$k_{17}$	∅		1.7–2.47
Grazers				
Maximum growth	$k_{63}$	day <sup>-1</sup>	0.04–0.44 <sup>a</sup> ; 0.1–0.76 <sup>b</sup>	0.43
Non-predatory mortality	$k_{64}$	day <sup>-1</sup>	0.005–0.16 <sup>a</sup> ; 0.005–0.155 <sup>b</sup> ; 0.001–0.155 <sup>h</sup>	0.1
Predatory mortality	$k_{69}$	day <sup>-1</sup>	0.001–0.1 <sup>b</sup>	0.01
Half-sat. for grazing	$k_{65}$	g C m <sup>-2</sup>		1.5
Temp. limitation	$\Theta_{GR}$	∅	1.07 <sup>i</sup>	1.07
Assimilation efficiency	$k_{66}$	g zoop C (g phyt C) <sup>-1</sup>	0.13–0.65 <sup>a</sup> ; 0.4–0.8 <sup>b</sup> ; 0.08–0.96 <sup>h</sup>	0.6

Literature data cited: <sup>a</sup>Jorgensen *et al.* (1991); <sup>b</sup>Bowie *et al.* (1985); <sup>c</sup>Sullivan *et al.* (2007); <sup>d</sup>Talling (1957); <sup>e</sup>Bissinger *et al.* (2008); <sup>f</sup>Jones (1977); <sup>g</sup>Megard (1972); <sup>h</sup>Collins & Wlosinski (1983); <sup>i</sup>Griffin *et al.* (2001).

significantly underestimated in some reaches (e.g. Caversham in Figure 3).

The upper reaches of the River Thames from the source to Hannington have a short residence time in the model simulations (0.5–3.5 days), and significant phytoplankton communities did not develop in the model. The model output showed that entrained dead organic matter represented the majority of the measured chlorophyll-*a*. Simulated high peaks in the middle–lower reaches of the Thames from Inglesham to Maidenhead comprised half SA and half EOM. In the lower reaches, abundant phytoplankton populations appeared when the optimal light and temperature conditions coincided with the long residence

time. The importance of the organic matter entrainment process decreased downstream. Residence time had an overwhelming importance on the simulated phytoplankton growth. During the medium–low-flow periods, the available light and the water temperature defined the community development. Grazing was an important phytoplankton growth limiting factor during the algae growth periods. In a scenario where grazers were not present in the system, the simulated chlorophyll-*a* concentrations increased by 30–100% in the phytoplankton growth periods.

Two examples for the longitudinal simulated chlorophyll-*a* concentrations are depicted in Figure 4. These two examples were selected because more than seven

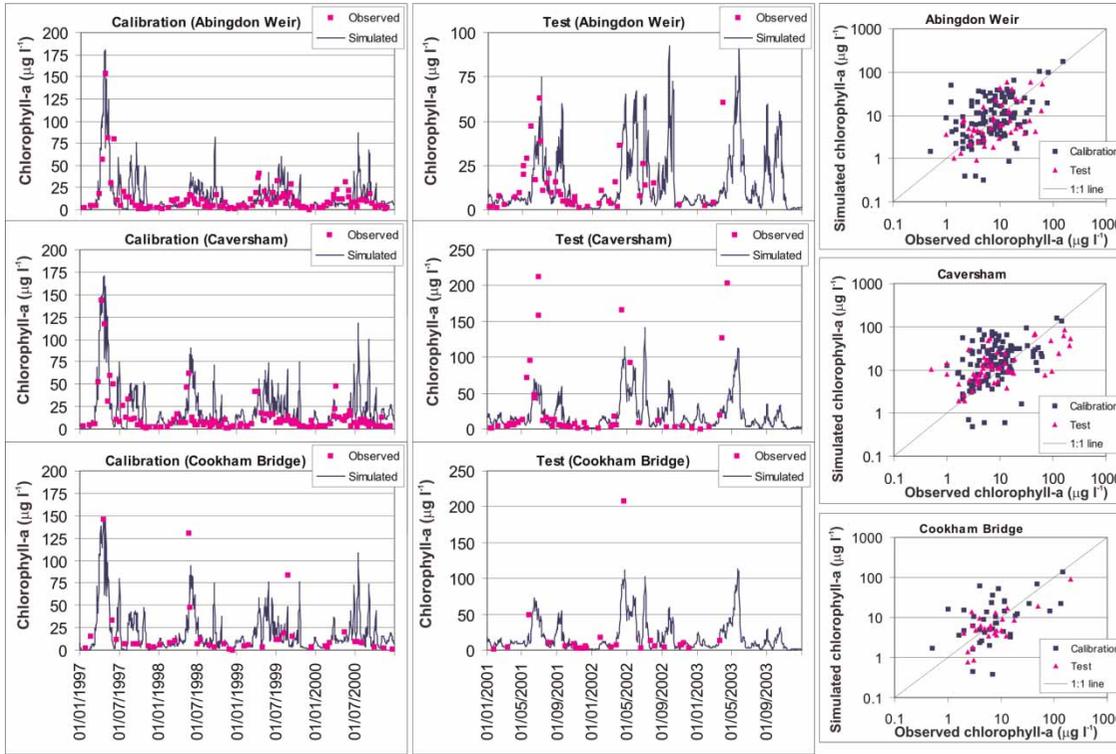


Figure 3 | Selected River Thames simulation results.

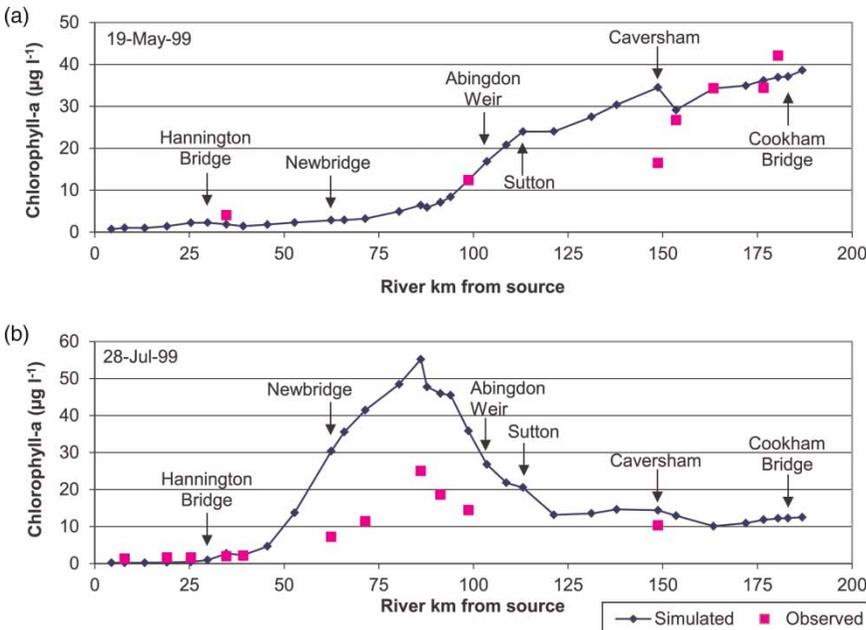


Figure 4 | Observed and simulated chlorophyll-a concentrations along the River Thames study area on (a) 19 May 1999 and (b) 28 July 1999.

observations were available on these days along the River Thames. The typical simulated distribution of chlorophyll-*a* concentrations along the River Thames is shown in Figure 4(a). On a typical day, the chlorophyll-*a* concentration increased gradually downstream. Three main sections were identified along the River Thames: (i) low chlorophyll-*a* concentrations from source to Newbridge; (ii) steep concentration increase between Newbridge and Sutton; and (iii) high concentrations with a moderate increase in concentration from Sutton to the end of the study area (Maidenhead). In some cases however, phytoplankton biomasses decreased slightly in between Days Lock and Sonning, which signifies the importance of local processes and conditions. The most significant increase in phytoplankton activity was simulated from Newbridge. Farmoor is located just downstream of Newbridge, where the Thames locking system starts. In the Newbridge–Sutton section of the Thames, the flow drops as a result of the locks and phytoplankton is ready to increase its population number when the environmental conditions are favourable. Downstream from Sutton, the general increase in concentration continues but at a lower rate.

The downstream transport of a phytoplankton bloom is captured in Figure 4(b). The simulated values are not at the level of the observed values, but the simulation captured the trend very well. Deviation from the observed values could be due to the uncertainty associated with the model structure and parameter set, but also from the observations (i.e. the grab samples represent only a moment, but the model simulates mean daily conditions). On this particular day (28 July 1999), all the environmental factors (water temperature, solar radiation and nutrients) were close to the optimum for algal growth; only the reach residence time limited their biomass increase.

All the available simulation and observation data are summarised in Figure 5 to assess the seasonality of phytoplankton. Obviously, there are much more simulation data than observations (18–119 observations per monitoring station versus 1,461 simulated values) and so the simulated and observed graphs are not identical. The figure shows the typical patterns along the River Thames.

It is clear that at Hunnington Bridge (30 river km from source) phytoplankton is always insignificant, although the observed values indicate this section as a potential source of an early season phytoplankton bloom (April). After

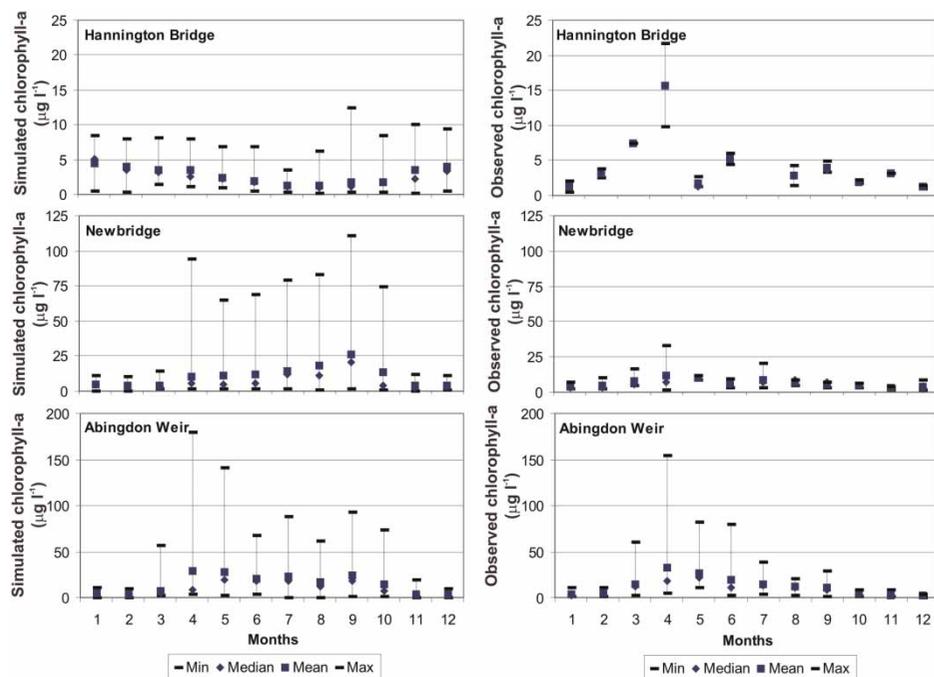
April, the adjacent trees probably shade the river surface and phytoplankton becomes light limited in the headwaters.

According to the model simulations, the next important river section is at Newbridge (at 62 river km from source), where the phytoplankton population sometimes significantly increase their biomass. The mean and median biomass (1997–2003) remains low in all months, but occasional bloom initiations are indicated by the high maximum values during April–October. The simulated mean/median chlorophyll-*a* concentrations generally increase from April to September. The observation dataset does not reflect these occasional high values, but only 60 observations were available for this monitoring station.

Finally, the phytoplankton biomass shows slightly different growth patterns for the lower reaches. At and downstream of Abingdon Weir (at 99 river km), both the simulated and observed chlorophyll-*a* concentrations are elevated and the spring concentrations tend to be higher than the late summer/early autumn concentrations. This is in contrast to the previously described behaviour at Newbridge. The reason might be the higher presence of algal grazers during the summer months. The observations at Abingdon Weir were similar to the simulated pattern, but the phytoplankton peaks were observed in the March–June period as opposed to the simulated results, where the highest peaks were simulated between March and October. Downstream of Abingdon Weir, the seasonality is the same but the concentration values are higher.

In general, the model results were comparable to the pattern of the observations. The August–September period was found to be the most vulnerable to phytoplankton blooms in the middle reaches, whereas the April–May period is the most important of the lower reaches in the River Thames.

The used model parameters fell within the range of the literature data (Table 1). It is clear that the phytoplankton growth rate was set to a moderate–low value ( $k_3$ ) but the natural mortality rate ( $k_4$ ) was close to the maximum value of the literature data. However, it was balanced with the high self-shading coefficient ( $k_7$ ), which allowed the production of large biomasses. The optimum water temperatures ( $T_{opt}$ ) and solar radiation ( $R_{opt}$ ) parameters represented the early spring, spring–autumn and summer conditions. The entrainment coefficients of dead organic matter indicated small background concentrations during low flows (small  $k_{16}$



**Figure 5** | Simulated and observed long-term monthly statistics (1997–2003) for three locations along the River Thames.

values), but large increases during storm events (large  $k_{17}$  values). The algal grazer population parameters indicate rapid fluctuation in the presence of grazers: high simulated grazer growth ( $k_{63}$ ) and natural mortality ( $k_{64}$ ). Predatory mortality of grazers ( $k_{69}$ ) was low (1%). These parameter values suggest that phytoplankton in the River Thames can be severely impacted by grazing (i.e. low algae growth rate, high grazer growth rate, low predatory mortality of grazers). This agrees with other studies suggesting that grazer populations in rivers consist of small-bodied zooplankton being able to grow rapidly in favourable conditions (Jones 1984; Wehr & Descy 1998). Significant phytoplankton populations, controlled to some extent by the presence of algal grazers, can therefore develop in the River Thames as a result of the long residence time.

## DISCUSSION

Our results show that phytoplankton was active from March to August with a peak in the April–May period. A low presence of phytoplankton was simulated between August and November, and negligible chlorophyll-*a* concentrations

were calculated during the winter months. This is in agreement with earlier studies by Young *et al.* (1999). Similarly to Young *et al.* (1999), this study also found that neither flow (i.e. insufficient residence time) nor phosphorus limited the phytoplankton growth in the Thames. However, our study shows that it is the combined effect of flow, water temperature and solar radiation variation that affects the timing and magnitude of chlorophyll-*a* peaks in the River Thames, although this magnitude is effectively mediated by the grazer population.

The average peak magnitude of the phytoplankton (*c.*  $75 \mu\text{g L}^{-1}$ ) in the River Thames is similar to other large rivers (Clout & Le Roux 1997; Sabater *et al.* 2008) and the observed maximum peak chlorophyll-*a* concentration ( $154 \mu\text{g L}^{-1}$ ) in the River Thames has a similar magnitude to previously reported values (Jones 1984). The phosphorus levels influenced by the diffuse and point pollution sources are mesotrophic in the upper reaches (source to Castle Eaton) and mesotrophic/eutrophic in the middle–lower reaches according to the suggested riverine classification of Dodds *et al.* (1998). Based on the same classification, the annual average chlorophyll-*a* concentrations indicate oligotrophic/mesotrophic conditions, but the low-flow

periods belong to the eutrophic category. The phytoplankton population were not controlled by these phosphorus levels in the model simulations. This agrees with the field observation of Neal *et al.* (2006), who suggested that the nutrient inputs should be further decreased to see an improvement in phytoplankton abundance. When the simulated chlorophyll-*a* concentrations are compared to the orthophosphate concentrations in the River Thames, it appears that nutrient concentrations might be controlled by the presence of large free-floating algal populations, i.e. orthophosphate levels are lower during large algal blooms as a result of the algal uptake and other in-stream processes (Picard & Lair 2005; Sabater *et al.* 2008; Neal *et al.* 2010a).

The model simulation in this study concluded that not only the residence time but also the light conditions and water temperature control the phytoplankton dynamics in the River Thames. This agrees with other studies on large rivers (Clout & Le Roux 1997; Picard & Lair 2005; Hilton *et al.* 2006). Algal grazers were also found to be important in sometimes significantly decreasing the phytoplankton population numbers. Just by themselves, however, they were unable to control the blooms. This again agrees with the findings of other studies (Griffin *et al.* 2001; Schöl *et al.* 2002).

Benthic processes (dead organic matter accumulation and benthic algae populations) were found to be important in the phytoplankton dynamics of the upper/middle reaches, which is also recognised in other studies (Reynolds & Descy 1996; Kowe *et al.* 1998; Wehr & Descy 1998). As a consequence of the long residence time of the study area sufficient doubling time is available to increase the planktonic algal population numbers which, together with the deepening river reaches (i.e. light limitation), reduces the importance of the benthic processes downstream. As a result, similarly to the River Continuum Concept (Vannote *et al.* 1980), phytoplankton numbers generally increase along the River Thames. However, localised conditions affected the phytoplankton development and dynamics in the simulation (i.e. chlorophyll-*a* concentrations steeply increase at Newbridge and slightly decrease, occasionally, between Days Lock and Sonning). This result highlights the importance of local processes in agreement with the results of Picard & Lair (2005) and Sabater *et al.* (2008), both of which emphasised the effect of local hydraulics

and other physical conditions on the phytoplankton development in large rivers.

## CONCLUSIONS AND WIDER COMMENT

A phytoplankton model was applied to the lowland River Thames. The model set-up was satisfactory in both the calibration and test periods. Based on modelling evidence, phytoplankton was controlled predominantly by the residence time of the water. In addition, the available light, water temperature and herbivorous grazing affected the River Thames phytoplankton population. In-stream nutrient concentrations (phosphorus) were not as important as these factors. These results support other observation-based studies (Neal *et al.* 2010c) and thus challenge the perceived importance of in-stream nutrient concentrations as the perceived primary control on phytoplankton growth and death in rivers. The observed and simulated seasonality of the phytoplankton was the same in the lower reaches of the River Thames (high spring, moderate summer, low autumn chlorophyll-*a* concentrations). The middle reaches of the River Thames had occasional high spring chlorophyll-*a* peaks, but the late summer months (August–September) more frequently resulted in higher concentrations. This simulated difference in the middle and lower reaches of the River Thames was explained by the presence and dynamics of the grazer population.

The present study builds on earlier modelling studies and was applied to a typical UK river basin influenced by farming and population constraints (Neal *et al.* 2010a). River systems that are strongly influenced by human intervention such as changing flow conditions, point and diffuse nutrient inputs will be affected by algal development and dynamics. Further, loss of riverine refuges as a result of management activities (e.g. weed cutting or pollution) may be significant as they influence the plankton-zooplankton dynamics, the role of grazers and their removal by fish.

Water management traditionally did not focus on aquatic ecology (Wehr & Descy 1998), but since the adoption of the EU Water Framework Directive (2000/60/EC), ecology became an essential part of the planning process. As a result river management has to balance social, ecological and economical needs under the currently changing climate (Wilby

*et al.* 2010). There are concerns about the sustainable management of rivers due to inevitable effects of human activities (Wehr & Descy 1998; Neal *et al.* 2006). Climate change is expected to increase the occurrence of phytoplankton blooms due to the decrease of summer flows, and increase in air and water temperatures. The situation with river systems is more complicated than for lakes because phytoplankton dynamics, and hence trophic status, do not correlate with water chemistry. The simple biomass-nutrient indicators hence do not work for rivers; phytoplankton dynamics is a result of the combined effects of physico-chemical changes and the biotic interactions (Wehr & Descy 1998). Wilby *et al.* (2010) emphasised the importance of adaptation strategies such as the plantation of riparian trees to shade and cool the river environment and the limited abstractions during low-flow periods. Scientific investigations of system behaviour can and water management planning must be supported by modelling evidence before action to be able to prioritise the available management options on a cost-benefit basis (Wehr & Descy 1998; Wilby *et al.* 2010). The carefully selected and applied mathematical models have potential to link the physical, chemical and ecological factors in a river system and within a catchment, which then can be compared to economic and social criteria. This not only improves the scientific understanding of the system behaviour, but also helps with the identification of critical factors and the selection of appropriate management strategies.

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