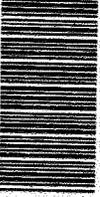


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On modeling the mechanisms that control in-stream phosphorus, macrophyte, and epiphyte dynamics: An assessment of a new model using general sensitivity analysis

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Abstract. The "Kennet model" is a new model of in-stream phosphorus (P) and macrophyte dynamics. Based on mass balance equations, the model represents the interactions between P and the suspended and bed sediments, the uptake of P by epiphytes and macrophytes, and the exchange of P between the water column and the pore water. The model simulates the total phosphorus (TP) and the soluble reactive phosphorus (SRP) concentrations observed in a reach of the River Kennet. Furthermore, the model simulates the generalized macrophyte growth patterns and total biomass observed in rivers throughout southern England. A general sensitivity analysis, based on Monte Carlo simulations and parameter values derived from the literature, identifies the key parameters controlling the model behavior when simulating macrophyte growth. The most important parameters are those that directly control macrophyte growth, those that define the epiphyte growth, and those that relate to the storage of P in the streambed.

1. Introduction

It is now widely accepted that phosphorus (P) is the major limiting nutrient in UK freshwater systems [Mainstone *et al.*, 2000]. As such, there are concerns regarding the effects of increased P loads to lakes and river systems, given that such increases can enhance the nutrient status of a water body and lead to excessive phytoplankton, macroalgae, and macrophyte growth. Such increases in growth often are viewed as a nuisance, particularly in conservation areas where certain plant species may grow at the expense of others, and often result in low oxygen concentrations, caused by the microbial breakdown of dead plant matter. These are detrimental to the invertebrate and fish populations [Fisher *et al.*, 1995]. Furthermore, the excessive growth of epiphytic algae restricts macrophyte development. Under low flow conditions the epiphytes, and the detritus that they trap, form a thick layer that shades the macrophyte's surface, thus restricting the rate of photosynthesis [Sand-Jensen, 1977; Phillips *et al.*, 1978].

The P in river and lake systems is derived from external and internal loads. External loads come from diffuse and point sources on the land surface. Within the UK the major diffuse sources result from the addition of fertilizer to crops and the wastes voided by farm animals, while the major point sources are derived from sewage treatment works (STWs) and industrial discharges. Internal loads are generated mainly from P released from sources within the water body such as the sediment and decaying organic matter [Golterman, 1975; House *et al.*, 1995]. Phosphorus is a highly reactive element, and the

dynamics of P transport both in the plant-soil system and within the aquatic environment are complex. Mathematical models are needed to aid the understanding of such systems as such models begin to link ideas of P transport and storage. Moreover, models are required to quantify the potential impacts of changing P loads on the water quality and ecology of aquatic environments. Such quantification is especially important for assessing the consequences of new or proposed legislation such as the Urban Wastewater Treatment Directive [Council of the European Community (CEC), 1991].

Models of lake systems have evolved from mass balance, steady state models [Vollenweider, 1975, 1976] to dynamic representations that account for sediment-water interactions, stratification [Chapra, 1997], and macrophyte dynamics [Asaeda and Van Bon, 1997]. More recently, the agricultural nonpoint source pollution model (AGNPS) and water quality analysis simulation program (WASP) models have been integrated to assess the temporal and spatial changes in external and internal P loads to a reservoir [Kao *et al.*, 1998]. Models of P loadings to rivers are also available, and these include the export coefficient method. This steady state model can be used to estimate the total P load in a water body from the sum of individual loads exported from separate land use types [Johnes, 1996]. However, while the model provides a relatively simple method of estimating the spatial variation in P loading at the national and international scale, it does not account for the effects of climate and hydrological flow paths. To some extent, this is addressed by the model of Gburek and Sharpley [1998], which models P export from source areas within a catchment and routes the export to the stream. At present the data intensity of this model limits its application to small research catchments. However, despite all these developments, a model that simulates the in-stream P dynamics and the associated feedbacks with macrophyte growth is required. Thus the aim of the work presented is to create a mathematical model of the principal mechanisms controlling the P and macrophyte dynamics in the rivers of southern England.

Detailed studies of macrophyte dynamics have been conducted in the chalk streams of England [Dawson, 1976; Wright

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et al., 1982]. On the basis of data gathered in the River Lambourn that illuminate the fundamental controls on macrophyte growth a conceptual model for such systems has been proposed [Ham *et al.*, 1981]. The specific objectives of the work reported here are to (1) create a generic mathematical model of P and macrophyte dynamics which conforms to the conceptual model of Ham *et al.* [1981], (2) to undertake a general sensitivity analysis (GSA) using Monte Carlo simulations to identify the key parameters controlling the model behavior, and (3) to check the simulated model output against observations of P concentrations and macrophyte growth observed in the rivers of southern England which drain chalk catchments, thereby testing the validity of the conceptual ideas.

2. Study Area

The model developed in this study is designed to be representative of Cretaceous Chalk catchments across southern and eastern England. This lithology is representative of large areas of lowland United Kingdom which drain carbonate aquifers and whose rivers are fed predominantly by groundwater (Figure 1). The chalk streams of southern England form important habitats for aquatic macrophytes, and the genus *Ranunculus* is particularly valued because of its attractive flowers and provision of shade to fish populations [Wright *et al.*, 1982].

The River Kennet (~1200 km²) is typical of a chalk catchment in southern England (Figure 1). Rising from a source at 190 m, the river flows broadly eastward for ~40 km before entering the River Thames at Reading. Cretaceous Chalk is fairly ubiquitous within the catchment and covers approximately 80% of the total area. The relief is dominated by gently sloping valleys, with the altitudinal range spanning 32 m at the confluence with the Thames, to 294 m at the highest point on the Marlborough Downs. The Kennet has two major tributaries: the Lambourn and the Enbourne. The catchment of the former is predominantly underlain by chalk, while that of the latter includes Tertiary Clay.

The long-term annual precipitation over the catchment is 774 mm, with approximately 38% ultimately apportioned to river flow and 62% apportioned to evapotranspiration. Much of the precipitation is percolated into the Chalk aquifer, and consequently, the flow response in streams is highly damped (except for the clay-lined Enbourne tributary). The long-term annual mean flow at Theale, the lowest gauging station on the Kennet, is 9.6 m³ s⁻¹ (or 294 mm of runoff), and the Q10 and Q95 flows are estimated as 16.6 and 3.8 m³ s⁻¹, respectively. The catchment is mainly rural, with arable agriculture being the predominant land use. There are several large towns along the main stem, and as such, treated sewage and industrial effluent are discharged directly into the Kennet. The catchment provides water for public and industrial supply by means of direct surface and groundwater abstractions. A substantial yield of 70–90 ML d⁻¹ is abstracted from the chalk aquifer by 33 boreholes arranged in seven well fields that make up the West Berkshire groundwater scheme. The balance between sewage inputs and river flow is subject to change in the English lowlands because of increasing urbanization, groundwater abstraction, and projected patterns of climate variability, leading to more extreme low-flow conditions [Neal *et al.*, 2000; Marsh and Sanderson, 1997]. The upper Kennet is the subject of an ongoing investigation, whose primary objective is to assess the impact of effluent from Marlborough STW on the receiving watercourse [Neal *et al.*, 2000]. Weekly water samples have

been taken from seven sites upstream of Knighton gauging station (Figure 1).

3. Methodology

3.1. Model Description

The new mathematical model describes the major factors and processes controlling P in river systems that have been reported in the literature. To perform the GSA, a generalized system behavior was described using macrophyte and water quality data gathered in studies of the Rivers Kennet and Lambourn [Dawson, 1976; Ham *et al.*, 1981; Neal *et al.*, 2000; Jarvie *et al.*, 2001a]. While the definitions of such behaviors are uncertain, the use of observed data provides the most reliable basis for defining the behaviors.

The model component describing the macrophyte growth pattern is based on the conceptual model of Ham *et al.* [1981], who identified discharge, solar radiation, dredging, and shading by epiphytic algae on the surface of plants as the most important factors controlling macrophyte growth. With regard to observations of the system behavior, Ham *et al.* [1981] also provided useful data. In the River Lambourn the *Ranunculus* generally was observed to begin growing rapidly in March until it reached a peak in August/September. On occasions a second period of growth has been observed in October, though this was small compared to the summer growth. During the winter months the macrophytes suffered extensive loss as the high discharges washed the plants away. The timing of the biomass peak changed with the prevailing flow conditions, further indicating a strong relationship between flow conditions and macrophyte biomass. This behavior was assumed to be typical of macrophytes in other chalk streams as similar behavior was observed elsewhere [Dawson, 1976; Wright *et al.*, 1982; Flynn *et al.*, 2001]. Using the water quality data collected in the upper reaches of the Kennet, it was also possible to define a reasonable range of stream water concentrations that may be expected in a chalk stream [Jarvie *et al.*, 2001a].

By generalizing the findings of the ecological and hydrochemical studies the following conditions were defined that represent the quantification of the processes implicit in the conceptual model of Ham *et al.* [1981]: (1) The peak macrophyte biomass must be greater than 50 gC m⁻² (135 g dry weight m⁻²) and less than 150 gC m⁻² (400 g dry weight m⁻²) [Dawson, 1976; Wright *et al.*, 1982; Flynn *et al.*, 2001]. (2) The peak macrophyte biomass must occur between August 1 and October 1 [Dawson, 1976; Wright *et al.*, 1982; Flynn *et al.*, 2001]. (3) The daily suspended sediment concentrations must be greater than 0.2 and less than 250 mg L⁻¹ [Jarvie *et al.*, 2001a]. (4) The mean annual pore water soluble reactive phosphorus (SRP) concentrations must be greater than 0.1 and less than 10 mg P L⁻¹. (5) The mean annual water column SRP concentrations must be less than 0.2 mg P L⁻¹ [Jarvie *et al.*, 2001a].

The mathematical model is a representation of the major stores in the aquatic P cycle and the in-stream processes that determine the transfer of P between those stores (Figure 2). At present the model is designed to simulate a single reach. The model is dynamic and operates on a daily time step. Moreover, it simulates the mean daily flow, total phosphorus (TP), soluble reactive phosphorus (SRP), boron and suspended sediment stream water concentrations in the water column, SRP concentrations in the pore water, and TP associated with the river bed sediments. In addition, the model simulates the resuspension of bed sediment, the deposition of suspended sediment,

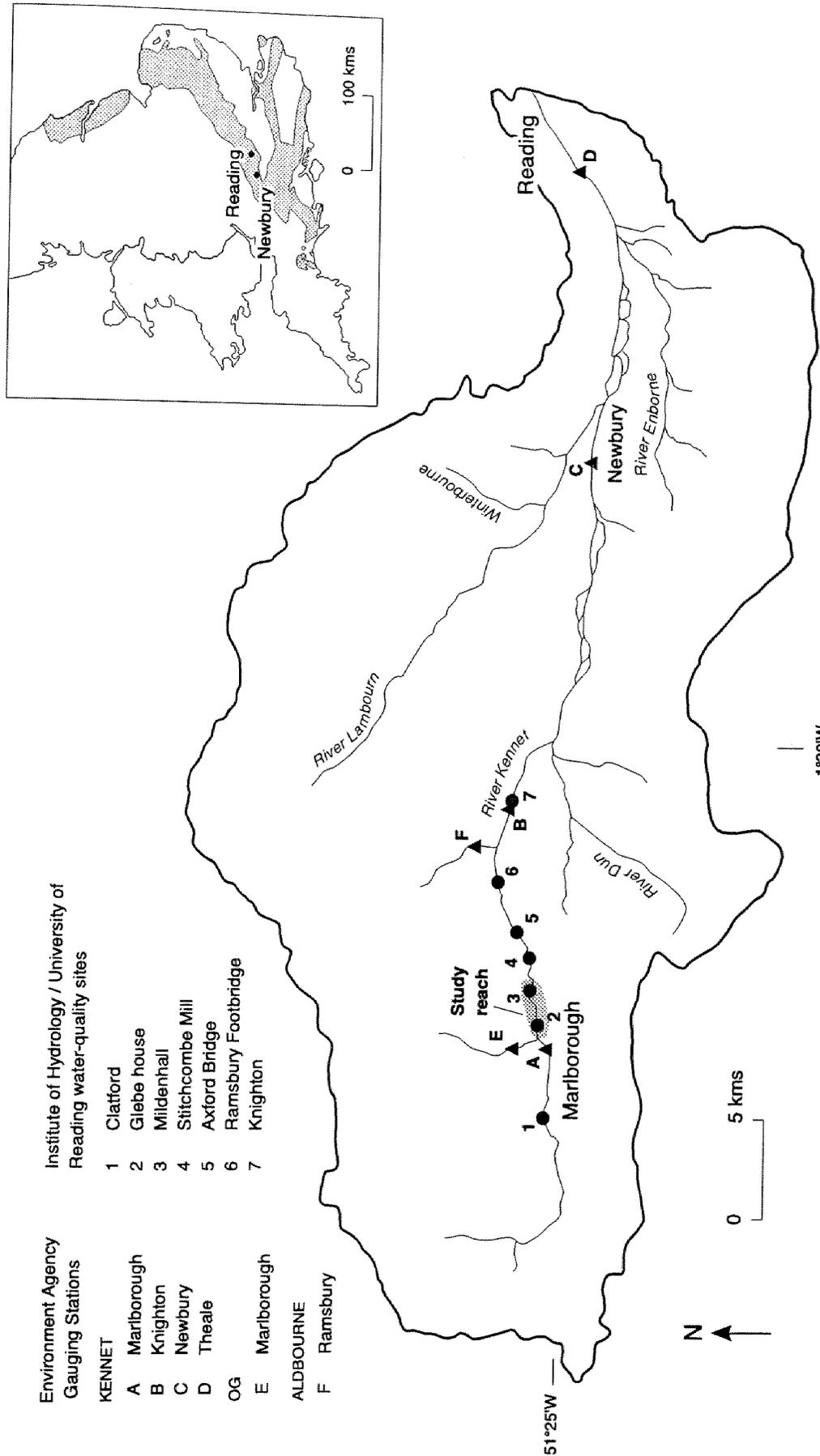


Figure 1. Schematic of the River Kennet catchment. The inset shows the location of Cretaceous Chalk within England.

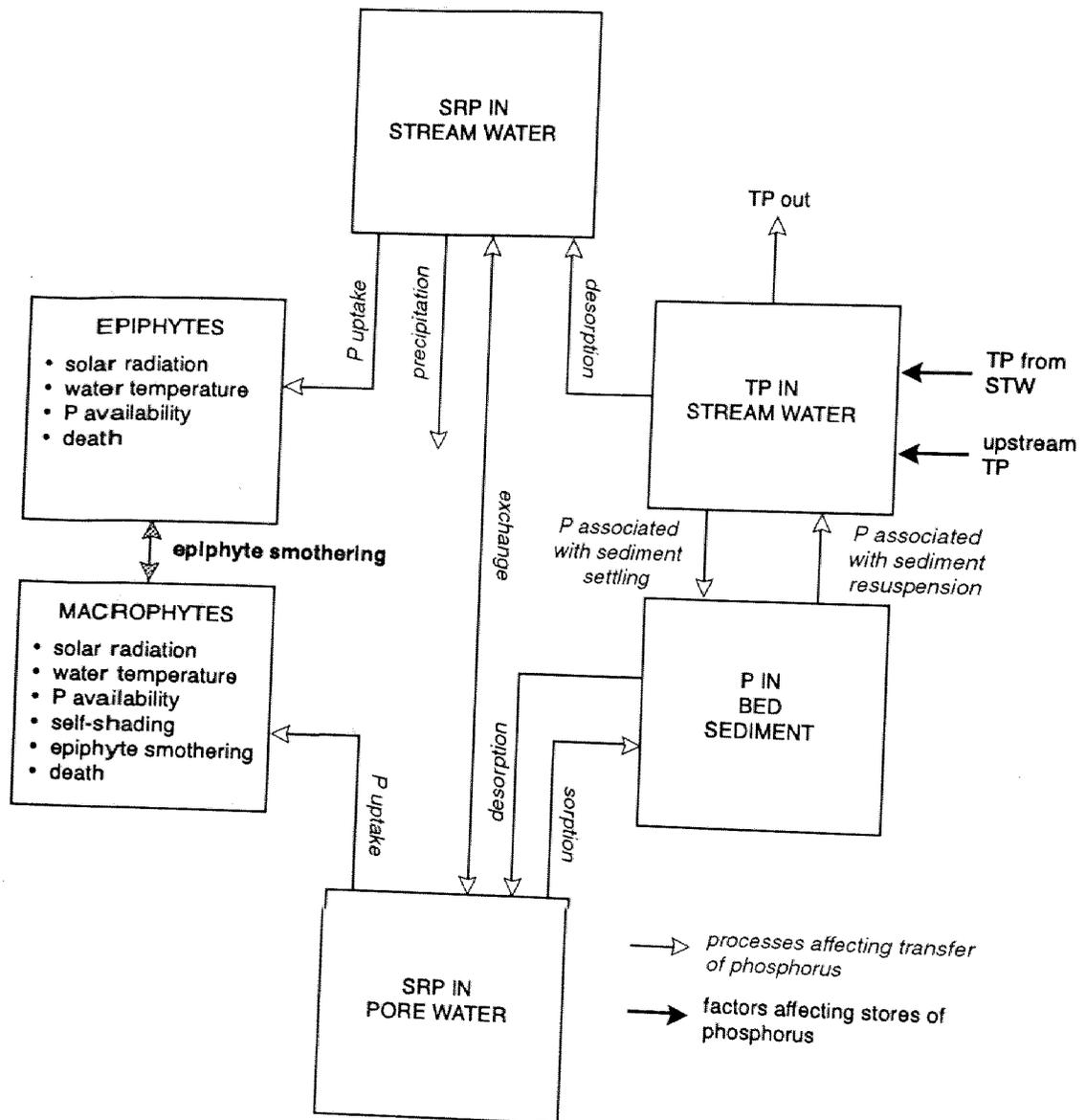


Figure 2. Schematic of the model of in-stream phosphorus dynamics showing the main stores and the transfer processes.

and the effects of the P concentrations on the growth of the macrophyte and epiphyte populations within the reach and the subsequent feedback that such growth has on the water column TP and SRP concentrations. Inputs to the model include measured and estimated time series data describing the flow, sediment, and P concentrations into the reach (Table 1). Stream water TP and SRP concentrations are simulated in this first instance because TP is a measure of the total amount of P in the system, and therefore is useful for mass balance, while SRP is a measure of the dissolved P in the stream water that is biologically available. Furthermore, SRP and TP concentrations are available for a site upstream of the STW input and at the end of the Mildenhall reach, and TP concentrations are available for the STW final effluent. It is assumed that TP is the sum of SRP + PP + SUP where PP is the particulate phosphorus and SUP is the soluble unreactive phosphorus.

Mass balance equations are used to quantify the amount of P (and carbon in the case of the macrophytes and epiphytes)

associated with the different stores in the aquatic P cycle (equations (1)–(22)). The rates of mass transfer between stores are modeled as first-order (linear) exchanges, and these rates are represented as parameters in the equations. However, while the equations are composed of linear exchanges, the combined response of feedbacks and temperature dependencies ensures that the response is nonlinear. The parameters and variables are listed in Tables 2 and 3, respectively. The linked differential equations are solved using a fourth-order Runge Kutta numerical integration algorithm with a variable step Merson integration routine. This ensures that the equations are solved accurately. The technique also has proved fairly stable with few numerical problems.

3.2. Model Differential Equations

The differential equation used to model the flow within the reach is

Table 1. Input Time Series and Constants

Input Variable	Description	Units	Measured/Estimated ^a
Time series			
u_1	flow into reach at time t	$\text{m}^3 \text{s}^{-1}$	E ^b
u_2	suspended sediment at time t	$\text{mg sediment L}^{-1}$	M
u_3	B in water column at time t	mg B L^{-1}	M
u_4	TP in water column at time t	mg P L^{-1}	M
u_5	flow into reach from STW at time t	$\text{m}^3 \text{s}^{-1}$	M
u_6	TP concentration in sewage effluent at time t	mg P L^{-1}	M
R	solar radiation at time t	normalized 0-1 ^c	M
T	water temperature at time t	$^{\circ}\text{C}$	M
u_9	lateral flow into reach at time t	$\text{m}^3 \text{s}^{-1}$	E ^b
u_{10}	B concentration in sewage effluent at time t	mg B L^{-1}	E ^d
B_{in}	total B concentration from all sources into reach at time t	mg B L^{-1}	M ^e
P_{in}	total TP concentration from all sources into reach at time t	mg P L^{-1}	M ^e
Constants			
L	reach length	m	M
w	reach width	m	M

^aM, measured data available for input. E, estimated values.

^bFlows estimated from measurements at nearest gauging stations.

^cOriginal time series of net radiation values (W m^{-2}) were normalized to the range 0-1 by dividing by the maximum value observed.

^dB effluent input estimated from mass balance within reach.

^e P_{in} and B_{in} are calculated from input time series using equations (7) and (12), respectively.

$$\frac{dx_1}{dt} = \frac{(u_1 + u_5 + u_9 - x_1)}{T_1}, \quad (1)$$

where x_1 is the flow out of the reach at time t ($\text{m}^3 \text{s}^{-1}$), u_1 is the upstream flow into the reach at time t ($\text{m}^3 \text{s}^{-1}$), u_5 is the STW flow into the reach at time t ($\text{m}^3 \text{s}^{-1}$), u_9 is the lateral inflow into the reach at time t ($\text{m}^3 \text{s}^{-1}$), and T_1 is the flow storage time constant (days).

Thus the changes in water storage in the reach are represented using a simple linear reservoir routing method, modified to account for the lateral and STW flow inputs. The time constant T_1 is estimated from the reach length L divided by the flow velocity v , which is itself estimated from the discharge using the expression $v = a(u_1 + u_5 + u_9)^b$, where a and b are constants. The values of a and b can be determined from flow-tracer experiments or from flow-velocity relationships derived at discharge gauging stations [Whitehead *et al.*, 1979].

Given that P is attached to both the suspended and bed sediments, it is necessary to estimate the amount of sorption and desorption between the P in the water and that associated with the suspended and bed sediments (Figure 2). To achieve this, an estimate of the mass of bed sediment is required. The bed mass is calculated from estimates of the reach length and width and an estimate of the depth of the material that could potentially be resuspended. This bed mass is modified, at each time step, by an estimate of the amount of material resuspended or deposited, and this amount is determined from the change in grain size with flow. Namely, a cumulative frequency curve for bed sediment has been measured in the River Lambourn, and therefore, for a given grain size, it is possible to estimate the fraction of the bed that is held in suspension.

The equation for the change in mean grain diameter of the bed material suspended at time t , x_9 (μm), is

$$\frac{dx_9}{dt} = c_1 \left(\frac{u_1 + u_5 + u_9 - x_1}{T_1} \right), \quad (2)$$

where c_1 is a constant relating the flow in the reach to the mean grain diameter resuspended or deposited from the overlying water column onto the streambed ($\mu\text{m s m}^{-3}$). It is

recognized that the change in grain diameter that is resuspended or deposited is a function of the shear velocity and the channel roughness [Chow *et al.*, 1988; Miller *et al.*, 1977]. However, a simple linear relationship between flow and grain diameter was used as a first approximation.

The change in grain size held in suspension was converted into a mass contribution to the suspended sediment concentration at time t , x_{10} ($\text{mg sediment L}^{-1}$), using the following equation:

$$\frac{dx_{10}}{dt} = \frac{1000}{V} \frac{d\text{PM}}{dx_9} \frac{dx_9}{dt}, \quad (3)$$

where V is the volume of water in the reach (m^3), PM is the potentially movable bed mass ($\text{kg } \mu\text{m}^{-1}$), and x_9 is the mean grain diameter of the bed material (μm).

The change in the potential available bed material with grain diameter is estimated using the equation $d\text{PM}/dx_9 = \Delta\text{CV}x_3wLf$, where ΔCV is the slope of the curve relating the cumulative fraction of the bed material to the grain size, x_3 is the total bed mass per m^2 , and f is the fraction of the total bed material that is available for resuspension. The factor of 1000 arises because of a unit conversion between kg m^{-3} and mg L^{-1} .

The equation for the suspended sediment x_2 ($\text{mg sediment L}^{-1}$) in the reach is

$$\frac{dx_2}{dt} = \frac{(u_2 - x_2)}{T_1} + \frac{1000}{V} \left(\frac{d\text{PM}}{dx_9} \right) \left(\frac{dx_9}{dt} \right) = \frac{(u_2 - x_2)}{T_1} + \frac{dx_{10}}{dt}, \quad (4)$$

where u_2 is the upstream suspended sediment concentration at time t ($\text{mg sediment L}^{-1}$).

The in-stream suspended sediment concentration is assumed to depend on the material that enters the reach, plus or minus that material which is resuspended or deposited, respectively. When (2) is negative, then the grain size held in suspension falls and the term becomes negative, thereby allowing the simulation of deposition in (4).

Table 2. Model Parameters

Parameter	Description	Units	Value or Range Given in or Derived From the Literature	Range Used in Monte Carlo Simulations	Reference
c_1	sediment resuspension/settling	$\mu\text{m s m}^{-3}$	1–10	5–50	est. ^a
c_2	pore water depth (multiplier)	[\emptyset]	0.25–0.45	0.25–0.45	est.
c_3	proportion of P in epiphytes	$\text{g P g}^{-1} \text{C}$	0.0054	0.0054 ^b	Dawson [1976]
c_4	epiphyte growth rate	$\text{m}^2 \text{g C}^{-1} \text{d}^{-1}$	0.004–0.04	0.004–0.04	Chapra [1997]
c_5	half saturation of P for epiphyte growth	mg P L^{-1}	0.0002–0.496	0.002–0.2	Bowie et al. [1985]
K_d^{sus}	K_d for suspended sediment	$\text{dm}^3 \text{kg}^{-1}$	200	100–300	Jarvie et al. [2001]
c_7	P exchange (water column/pore water)	d^{-1}	0.4–86.4	0.3–3.0	Wagner and Harvey [1997]
c_8	precipitation of P in water column	d^{-1}	0.68	0.35–1.05	House et al. [1995]
c_9	K_d for bed sediment (as a fraction of K_d^{sus})	[\emptyset]	0.1–1.0	0.1–1.0	Jarvie et al. [2001]
c_{10}	macrophyte growth rate	d^{-1}	0.1–0.8	0.2–0.6	Dawson [1976]
c_{11}	half saturation of P for macrophyte growth	mg P L^{-1}	0.0002–0.496	0.002–0.2	and Wright et al. [1982] Bowie et al. [1985]
c_{12}	self-shading bed (bulk)	g C m^{-2}	74	10–50	Dawson [1976]
c_{13}	sediment depth	m	0.1–1.0	0.1–1.0	est.
c_{14}	macrophyte death rate	$\text{s g C}^{-1} \text{d}^{-1}$	0.01–0.3	0.01–1.0	Chapra [1997]
c_{15}	proportion of P in macrophytes	$\text{g P g}^{-1} \text{C}$	0.0054	0.0054 ^b	Dawson [1976]
c_{16}	epiphyte death rate	$\text{s d}^{-1} \text{m}^{-3}$	0.01–0.05	0.01–0.05	Bowie et al. [1985]
θ_M	macrophyte temperature dependency	[\emptyset]	1.01–1.066	1.006 ^b	Bowie et al. [1985]
θ_E	epiphyte temperature dependency	[\emptyset]	1.01–1.066	1.066 ^b	Bowie et al. [1985]
n	porosity	[\emptyset]	0.3	0.3 ^b	Chow et al. [1988]
ρ_s	bulk sediment density	kg m^{-3}	2.65	2.65 ^b	Chow et al. [1988]
a	velocity-flow parameter	m^{-2}	0.18	0.18	est.
b	velocity-flow parameter	[\emptyset]	0.68	0.68	est.
f	fraction of the total bed material that is available for resuspension	[\emptyset]	0.0–1.0	0.1	est.

^aHere, est., parameter values estimated through calibration and expert knowledge.

^bModel parameters fixed with a single value for model simulations since the literature suggested that these were the most appropriate values.

The change in moveable bed mass at time t , x_3 (kg sediment m^{-2}), is expressed using the following equation:

$$\frac{dx_3}{dt} = \frac{1}{Lw} \left(\frac{d\text{PM}}{dx_9} \right) \frac{dx_9}{dt}, \quad (5)$$

where all the terms have been defined previously. The equation is an expression of the mass of sediment that is gained or lost from the bed following the resuspension or deposition of sediment. The change in the TP in the water column at time t , x_4 (mg P L^{-1}), is represented by the following equations:

$$\frac{dx_4}{dt} = \frac{(P_{\text{in}} - x_4)}{T_1} - \frac{c_3 c_4 x_8 x_7 R x_{11} \theta_E^{(T-20)} w a}{(u_1 + u_5 + u_9)^{1-b} (c_5 + x_{11})} + c_7 (x_{12} - x_{11}) - c_8 x_{11} + \left\{ \begin{array}{l} \text{GAIN} \\ \text{LOSS} \end{array} \right\}, \quad (6)$$

where

$$P_{\text{in}} = \frac{(u_4 u_1 + u_6 u_5 + 0.016 u_9)}{(u_1 + u_5 + u_9)}, \quad (7)$$

Table 3. Model Outputs

Variable	Description	Units
x_1	flow out of reach at time t	
x_2	suspended sediment at time t	$\text{m}^3 \text{s}^{-1}$
x_3	moveable bed load at time t	$\text{mg sediment L}^{-1}$
x_4	TP in water column at time t	$\text{kg sediment m}^{-2}$
x_5	B in water column at time t	mg P L^{-1}
x_6	TP in pore water at time t	g P m^{-2}
x_7	macrophyte biomass at time t	mg P L^{-1}
x_8	epiphyte biomass at time t	g C m^{-2}
x_9	grain diameter suspended	g C m^{-2}
x_{10}	concentration of sediment resuspended or settled	μm
x_{11}	SRP in water column at time t	$\text{mg sediment L}^{-1}$
x_{12}	SRP in pore water at time t	mg P L^{-1}
T_1	residence time of water in reach at time t	mg P L^{-1} day

$$\text{GAIN} = + \frac{1}{\rho_s(1-n)} x_6 \frac{dx_{10}}{dt} 10^{-3}, \quad (8)$$

$$\text{LOSS} = + K_D^{\text{sus}} x_{11} \frac{dx_{10}}{dt} 10^{-6}, \quad (9)$$

where P_{in} is the total concentration of P entering the reach at time t (mg P L^{-1}), u_4 is the upstream TP concentration of the water flowing into the reach at time t (mg P L^{-1}), u_6 is the TP concentration entering the reach at time t from the STW (mg P L^{-1}), 0.016 is the estimated TP concentration of the water flowing into the reach at time t from lateral inflow (mg P L^{-1}), c_3 is the ratio of phosphorus to carbon in epiphytes (g P g C^{-1}), c_4 is the epiphyte growth rate ($\text{m}^2 \text{g C}^{-1} \text{d}^{-1}$), c_5 is the half-saturation constant associated with the epiphyte growth (mg P L^{-1}), c_7 is the constant associated with the exchange of SRP between the pore water and the overlying water column (d^{-1}), c_8 is the constant associated with the coprecipitation of P with calcite in the water column (d^{-1}), R is solar radiation; x_6 is the TP concentration associated with the bed sediment (mg P L^{-1}), x_7 is total macrophyte biomass (gC m^{-2}), x_8 is total epiphyte biomass (gC m^{-2}), x_{11} is the SRP concentration in the water column (mg P L^{-1}), x_{12} is the SRP concentration in the pore water (mg P L^{-1}); θ_E is epiphyte temperature dependency ($[\theta]$), T is water temperature ($^{\circ}\text{C}$), $K_D^{\text{sus}} = K_d$ for suspended sediment ($\text{dm}^3 \text{kg}^{-1}$), $K_D^{\text{bed}} = K_d$ for bed sediment ($\text{dm}^3 \text{kg}^{-1}$), n is the porosity (\emptyset), and ρ_s is the bed sediment bulk density (kg m^{-3}). The K_d values are a measure of the affinity of the solid phase for sorbing P from the surrounding substrate [House et al., 1995; House and Warwick, 1999].

It is assumed that the TP concentration of the water column is determined by the amount of phosphorus entering the reach (from both upstream and the STW), epiphyte uptake, sorption/desorption of P to and from the suspended sediment, exchange of P between the pore water and water column, and the precipitation of P (Figure 2). As such, the estimate of the change in the TP concentration is based only on changes in the PP and SRP: It is assumed that any SUP present, by definition, does not take part in any reactions.

The TP concentration input to the reach is calculated from the mass balance of all the known P sources: upstream, STW, and lateral flow inputs (equation (7)). The first term on the right-hand side of (6) represents the input and storage of total phosphorus within the reach. The second term represents the uptake of SRP by the epiphytic algae. As such, the term is described in more detail with reference to epiphyte biomass equation (18). The multiplication factor of

$$\frac{c_3 w a}{(u_1 + u_5 + u_9)^{1-b}},$$

which is an expansion of the expression c_3 divided by the depth of the water column (which varies with flow), converts the epiphyte biomass into an equivalent mass of phosphorus per liter of water. The third term on the right-hand side of (6) represents the exchange of SRP between the pore water and the overlying water column. When the pore water concentration is greater than that of the overlying water column, then there is a net transfer of SRP to the overlying water column. Conversely, if the SRP concentration is greater in the overlying water column compared to the pore water, then SRP is transferred to the pore water. The fourth term represents the loss of SRP from the water column by coprecipitation with calcite. The final term represents the loss of total phosphorus from the water column to the streambed by sediment deposition or the gain of PP from the bed during periods of resuspension. Given that dx_{10}/dt can be both positive and negative, then the sign represents the addition or subtraction of PP from the TP store in the water column. It is assumed that PP in suspension in the water column is in equilibrium with the surrounding SRP in the water column and that the PP associated with the streambed is in equilibrium with the surrounding SRP in the pore water. The gain and loss terms reflect these equilibrium conditions, which are expressed in terms of K_d values. It is assumed that $K_D^{\text{bed}} \leq K_D^{\text{sus}}$, since the sediment in suspension will sorb more SRP than the bed sediment. For the purposes of estimating suitable values for K_D^{bed} and K_D^{sus} both are assumed to lie in the range 100–300 $\text{dm}^3 \text{kg}^{-1}$, which is the range specified for bed sediment by Jarvie et al. [2001a]. As such, K_D^{sus} is chosen from this range, and K_D^{bed} is estimated as a fraction, c_9 (0.1–1.0), of K_D^{sus} . Namely,

$$K_D^{\text{bed}} = c_9 K_D^{\text{sus}}. \quad (10)$$

Boron (B), which is predominantly derived from STW, is used as a tracer with which to evaluate changes in in-stream P concentrations following STW effluent treatment [Neal et al., 2000]. Hence B is included in the model, and the equation for the change in the concentration, x_5 (mg B L^{-1}), in the reach is

$$\frac{dx_5}{dt} = \frac{B_{\text{in}} - x_5}{T_1}, \quad (11)$$

where

$$B_{\text{in}} = \frac{(u_1 u_3 + u_5 u_{10})}{u_1 + u_5 + u_9}, \quad (12)$$

where B_{in} is the total concentration of P entering the reach at time t (mg B L^{-1}), x_5 is the B concentration in the water column (mg B L^{-1}), u_3 is the upstream B concentration into the reach at time t (mg B L^{-1}), and u_{10} is the B concentration entering the reach at time t from the STW (mg B L^{-1}).

It is assumed that the B within the reach is entirely STW derived and there is no B in the lateral inflow [Neal et al., 2000]. Boron is also assumed to be conservative; as such, it does not take part in any reactions within the river reach and can be modeled using a simple input-output mass balance equation.

The equation for the change in the TP associated with the river bed, x_6 (mg P L^{-1}), in the reach is

$$\frac{dx_6}{dt} = - \left\{ \begin{array}{l} \text{GAIN} \\ \text{LOSS} \end{array} \right\} - c_7(x_{12} - x_{11})n - \frac{c_{15}c_{10}\theta_M^{(T-20)}x_7x_{12}Rc_{12}}{p(c_{11} + x_{12})(c_{12} + x_7)} n \quad (13)$$

where

$$\text{GAIN} = +10^{-6}x_{11}K_D^{\text{sus}} \frac{dx_{10}}{dt} \frac{(u_1 + u_5 + u_9)^{1-b}}{wa} \frac{1}{c_{13}}, \quad (14)$$

$$\text{LOSS} = +10^{-3}x_6 \frac{1}{p_s(1-n)} \frac{dx_{10}}{dt} \frac{(u_1 + u_5 + u_9)^{1-b}}{wa} \frac{1}{c_{13}}, \quad (15)$$

where c_{10} is the macrophyte growth rate ($\text{m}^2 \text{g C}^{-1} \text{d}^{-1}$), c_{11} is the half-saturation constant associated with the macrophyte growth (mg P L^{-1}), c_{12} is the constant associated with macrophyte self-shading (g C m^{-2}), c_{13} is the bulk sediment depth, c_{15} is the ratio of phosphorus to carbon in macrophytes (g P g C^{-1}), and p is the pore water depth (m).

It is assumed that the TP associated with the river bed is affected by three factors. The first is the mass of phosphorus sorbed on the bed sediment. As such, the gain and loss term on the right-hand side of (13) represents the movement of PP between the streambed and the overlying water column due to deposition (a gain of PP to the streambed) and resuspension (a loss of PP from the streambed). The second factor is the interaction between the SRP associated with the pore water and the overlying water column. The third is uptake of SRP from the pore water during periods of macrophyte growth. The pore water depth p cannot be greater than the bulk sediment depth. As such, the pore water depth is estimated as a fraction, c_2 , of the bulk sediment depth c_{13} . Namely,

$$p = c_2c_{13}. \quad (16)$$

The differential equation used to model the change in the macrophyte biomass, x_7 (g C m^{-2}), flow within the reach is

$$\frac{dx_7}{dt} = \frac{c_{10}\theta_M^{(T-20)}x_7x_{12}Rc_{12}}{(c_{11} + x_{12})(c_{12} + x_7)} - c_{14}x_7x_8x_{11}, \quad (17)$$

where θ_M is macrophyte temperature dependency ($[\theta]$) and c_{14} is the macrophyte death rate ($\text{m}^2 \text{g C}^{-1} \text{d}^{-1} \text{m}^{-3} \text{s}^{-1}$).

The general form of (17), which simulates the interactions between the macrophytes and the epiphytic algae, is based on the Lotka-Volterra model of predator-prey interactions [Lotka, 1926; Volterra, 1926]. In this case, the macrophytes are considered as the "prey," and the epiphytic algae are considered as the "predator." While the coexistence of macrophytes and epiphytes is not a true predator-prey relationship, the Lotka-Volterra model does generate the expected relational

changes in biomass. Unmodified formulations of the original Lotka-Volterra predation model have been shown to produce peak biomass estimates that are mainly dependent on the initial conditions [Hastings, 1997]. As such, the basic Lotka-Volterra model has been modified as follows. The first-order growth rate c_{10} is also dependent on the substrate (water column) SRP concentration [Thornley, 1976]. This dependency is described by the Michaelis-Menten formulation, in which the half-saturation constant c_5 represents the substrate concentration at which growth is half the maximum. As such, the parameter dictates at what level the substrate becomes limiting. The term for the macrophyte growth also is modified to account for the seasonal variations in solar radiation and water temperature. The conversion ratio of P:C relates the mass of P removed from the pore water by the macrophytes to the biomass increase, which is measured in terms of carbon [Dawson, 1976].

The second term, which includes the product of the macrophyte and epiphyte biomass, x_7x_8 , on the right-hand side of equation, quantifies the effect the impact of the epiphytic algae has on the macrophyte mortality. This term is also flow dependent to account for the washout of macrophytes from the reach under high-flow conditions.

The equation for the change in the epiphyte biomass x_8 (g C m^{-2}) in the reach is

$$\frac{dx_8}{dt} = \frac{c_4\theta_E^{(T-20)}x_8x_7Rx_{11}}{(c_5 + x_{11})} - c_{16}x_8x_{11}, \quad (18)$$

where c_{16} is the epiphyte death rate ($\text{d}^{-1} \text{m}^{-3} \text{s}^{-1}$).

The term $(c_4\theta_E^{(T-20)}Rx_{11})/(c_5 + x_{11})$ quantifies the epiphyte growth. As in the case of the macrophytes it is based on the Michaelis-Menten formulation with a dependency upon the SRP available in the pore water and water column, respectively, and the water temperature and solar radiation. The death rate of the epiphytes is also flow dependent.

The SRP water column concentration x_{11} (mg P L^{-1}) in the reach is derived from the mass balance of the different forms of P.

$$\text{TP} = \text{PP} + \text{SRP} + \text{SUP}, \quad (19)$$

where TP is total phosphorus concentration (mg P L^{-1}), PP is particulate phosphorus concentration (mg P L^{-1}), SRP is soluble reactive phosphorus concentration (mg P L^{-1}), and SUP is soluble unreactive phosphorus concentration (mg P L^{-1}).

On the basis of data gathered in the River Lambourn it is assumed that 25% of TP is SUP [Prior, 1999]. While this percentage is known to change with the prevailing flow conditions, the assumption was made so that SUP concentration data are not required to apply the model given that these data are generally unavailable, whereas TP and SRP data tend to be collected by the Environment Agency at routine monitoring sites. Thus

$$\text{TP} = \text{PP} + \text{SRP} + 0.25\text{TP}. \quad (20)$$

Substitute $\text{PP} = \text{SRP} \times 10^{-6} K_D^{\text{sus}} x_2$ and rearrange (where $\text{TP} = x_4$ and $\text{SRP} = x_{11}$)

$$x_{11} = \frac{0.75x_4}{1 + (10^{-6}K_D^{\text{sus}}x_2)}. \quad (21)$$

By the same arguments used to derive (21), the equation for the change in the SRP pore water concentration x_{12} (mg P L^{-1}) in the reach is

$$x_{12} = \frac{0.75 \cdot x_6}{1 + \frac{K_D^{\text{bed}}}{p} 10^{-3} x_3}, \quad (22)$$

where the PP is given by

$$\text{PP} = x_{12} \frac{K_D^{\text{bed}}}{p} \times 10^{-3} x_3$$

in this case. If SUP (or the equivalent dissolved hydrolysable P, DHP) concentration data are available, then the values could be substituted in (20).

3.3. General Sensitivity Analysis

A general sensitivity analysis (GSA) was undertaken to identify the key model parameters controlling the macrophyte growth pattern. This pattern is of particular interest for two reasons. First, there is concern regarding the conservation of *Ranunculus* within the reach, and second, the macrophyte growth is the integrated result influenced by all the model equations. The GSA was based on the utilization of the model together with a classification algorithm. The general system behavior was defined by the five criteria previously outlined in section 3.1. A classification algorithm was coded into the mathematical model to allow the model output to be identified as either representative or not representative of the generalized behavior criteria. The idea of the GSA was to inject uncertainty into the model by randomly selecting the model parameters from uniform probability distributions rather than experimentally derived values. This was achieved using a Monte Carlo technique in which the model was run using a set of parameters drawn randomly from the distributions. Having completed the simulation, the results were stored, and the process was repeated 10,000 times [Spear, 1970]. Uniform probability distributions were chosen so that each parameter value had an equal chance of being chosen. The range of the parameter distributions was determined from values derived from the available literature, although six parameters were held constant as their values were well defined (Table 2).

Each simulation result consisted of the parameter vector itself and the behavioral outcome: whether the particular parameter vector gave rise to the behavior or not (i.e., nonbehavior). Namely, the final result of the 10,000 simulations is m parameter vectors that led to behavior and $n = (10,000 - m)$ which did not. The final results were analyzed statistically to identify the key parameters causing the model to reproduce the observed behavior. The theory behind this statistical analysis is based on the separation between the cumulative probability distributions, and a Kolmogorov-Smirnov two-sample test is utilized to assess the separation [Hornberger and Spear, 1980; Spear and Hornberger, 1980]. The statistic $d_{m,n}$ is determined as the maximum vertical distance between the cumulative probability distribution curves for m behaviors and n nonbehaviors (e.g., Figure 3). Thus large values of $d_{m,n}$ indicate that the parameter is important for simulating behavior. The cumulative frequency curves also highlight if the values of the parameters causing the behaviors were at the lower or upper bounds or around the midpoint of the range. Successive runs of 10,000 simulations were done with the parameter ranges adjusted between runs so as to increase the number of behaviors to a level sufficient for the statistical analysis [Spear and Hornberger, 1980; Whitehead and Hornberger, 1984].

For each model run, the reach between the STW just up-

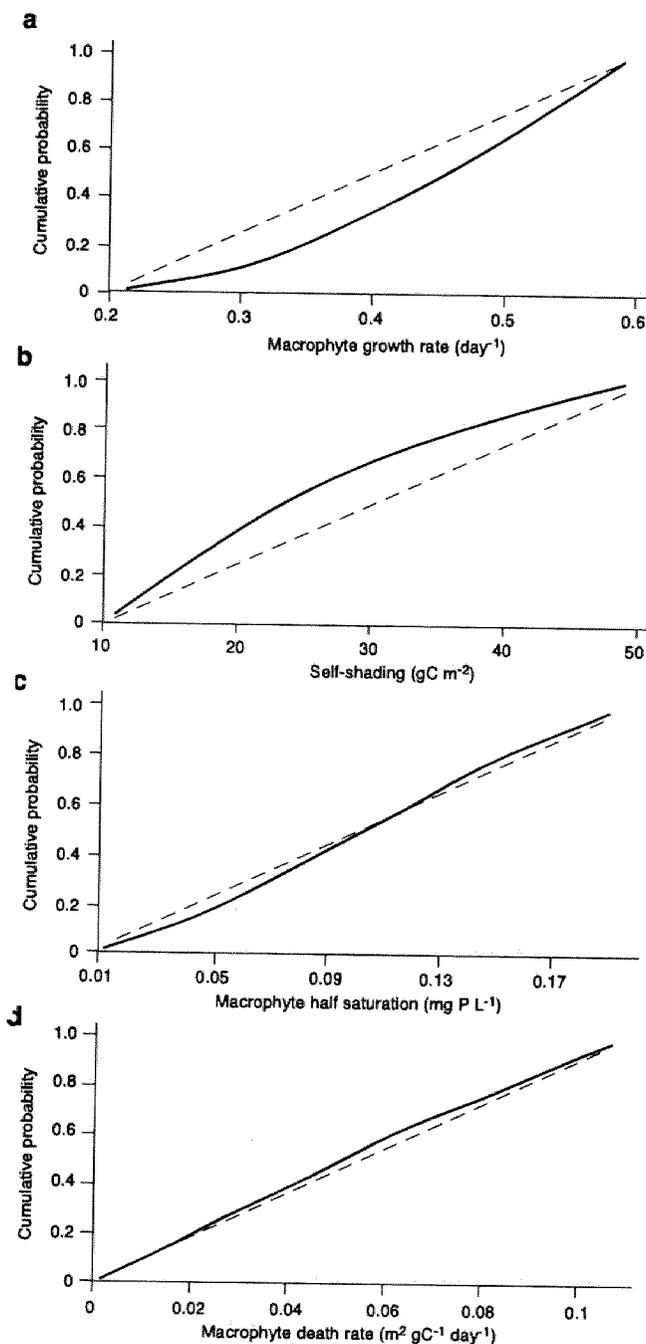


Figure 3. Cumulative distribution functions under the behavioral mapping for parameters. These functions exhibit three forms. The first is a mean shift, exhibited by (a) macrophyte growth rate and (b) macrophyte self-shading, which both show distinct separation. The second is a variance shift, exhibited by (c) macrophyte half saturation. The third is no separation, exhibited by (d) macrophyte death rate. The solid and dashed lines represent the behaviors and nonbehaviors, respectively.

stream of site 2 and site 3 was simulated over a 2-year period with a daily time step (Figure 1). The input data used to drive the model were derived from water quantity and quality data sets collected by the Environment Agency and Centre for Ecology and Hydrology, Reading University, respectively. No observed flow data were available for the reach; therefore input flows were estimated from the four nearest gauging stations at Marlborough (on the River Kennet and River Og), Ramsbury,

and Knighton. The flow in the reach was estimated from a mass balance calculation using the mean daily flow observed at each gauging station (Figure 1). Essentially, the flow between Knighton and Marlborough was estimated using the mass balance equation. This in-reach flow could then be weighted by length to provide an estimate of the groundwater input. This estimate also was adjusted for the influence of lateral inflow, the input from Marlborough STW, and groundwater abstraction from Axford. The latter two influences are monitored by Thames Water.

Weekly water samples were taken from seven sites upstream of Knighton gauging station between January 1998 and December 1999 [Neal *et al.*, 2001; Jarvie *et al.*, 2001a] (Figure 1). The furthest upstream site was Clatford, which was upstream of Marlborough STW. Another site, at Glebe House, was located immediately downstream of the STW, and the site at Mildenhall was a further 1.5 km downstream of the STW. The water quality samples were analyzed for a broad range of determinands, including suspended sediment, B, SRP, and TP [Jarvie *et al.*, 2001a]. From November 1998 to March 1999, daily TP concentrations were measured at Clatford and Mildenhall. TP concentrations from the STW also were available from Thames Water. Furthermore, daily solar radiation and water temperature data were measured in the reach using an automatic weather station and Hydrolab, respectively.

Since stream water and STW chemistry data were only available with a resolution of one week at best (except for the period between November 27, 1998, and March 23, 1999, when daily samples of TP were available), then, to generate a daily time series, one data value was copied forward in time until the next observation was made. While this obviously limits the resolution of the model to determining the weekly dynamics of the system, it represents a pragmatic response to data scarcity. Furthermore, the basic structure of the model remains unchanged, so that if daily data are available then they can be used. To run the model, it also is necessary to specify the initial conditions for each of the differential equations. In the case of flow, suspended sediment, TP, and B for the stream water, macrophytes, and epiphytes, the initial values could be estimated from observed data for December 31, 1997. The bed load and the grain size were estimated from studies of the River Lambourn by D. E. Evans (unpublished results, 1998) and the pore water TP concentrations from initial measurements made by W. A. House (unpublished results, 1998). The behavior criteria did not include the first 30 days of simulated output, so the effects of the initial conditions on the results were minimized.

Following the simulations using the five criteria defined in section 3.1, the Monte Carlo simulations were run twice more, but with changed behavior criteria. In the first instance, criteria 2–5 were retained, but the macrophyte criterion (criterion 1) was replaced by the following two criteria: In criterion 6, the peak macrophyte biomass must be greater than 50 g C m^{-2} and less than or equal to 75 g C m^{-2} in both years 1 and 2. In criterion 7, the peak macrophyte biomass must be greater than 75 g C m^{-2} and less than or equal to 150 g C m^{-2} in both years 1 and 2.

Thus three sets of behavior were produced: those that fit criteria 2–6, those that fit criteria 2–5 and 7, and the nonbehaviors. The aim of these simulations was to try to identify the parameters controlling the size of the macrophyte biomass peak. In the second instance, further simulations were done

Table 4. Model Parameters Significant at 95% Level (0.051) or Greater

Parameter	Description	$d_{m,n}$
c_{12}	macrophyte self-shading	0.194
c_{10}	macrophyte growth rate	0.183
c_4	epiphyte growth rate	0.177
c_{16}	epiphyte death rate	0.137
c_{11}	macrophyte half saturation	0.068
K_d^{sus}	K_d for suspended sediment	0.060
c_5	epiphyte half saturation	0.059
c_{13}	bulk sediment depth	0.054

using only the P behavior criteria (criteria 3–5) to determine the primary controls on the stream water TP concentrations.

4. Results

The 10,000 simulations produced 769 outputs in the behavior defined by criteria 1–5 and 9231 in the nonbehavior categories, respectively.

4.1. Kolmogorov-Smirnov (K-S) Test

The parameters and the corresponding $d_{m,n}$ statistics that are significant above the 95% level are listed in Table 4. The parameters listed are mainly those directly controlling the biomass of macrophytes, such as the macrophyte and epiphyte growth rates. The epiphyte growth is important as it determines the biomass of the epiphytes and therefore the extent to which they impact the macrophyte growth. Other important parameters include the self-shading and half-saturation constants, which also define the limits to growth, and bulk sediment depth and the K_d^{sus} value, which control the amount of available P in the bed sediment and the sorption/desorption of P from suspended sediment, respectively.

Some examples of the differences between behavior and nonbehavior cumulative frequency curves are shown in Figures 3a–3d. The cumulative frequency curve for the macrophyte growth rate parameter shows that the most behaviors occur at the higher values in the range (Figure 3a). Conversely, values at the lower end of the range give the most behaviors for the macrophyte self-shading (Figure 3b). The curve for the macrophyte half saturation shows that most of the behaviors occur when the parameters have values in the middle of the range (Figure 3c). When the parameter is not determining if a behavior is achieved or not, then the two cumulative frequency curves for behaviors and nonbehaviors are broadly similar with no statistically significant separation between them (Figure 3d). An example of such a parameter in this application is the macrophyte death rate, which is not important in these simulations because of the definition of the behavior criteria: It was not specified when, or how rapidly, the macrophyte biomass should have fallen to its minimum value in the year.

The majority of the model parameters were independent. The most significant correlations are shown in Table 5. The largest correlation (of 0.73) was between macrophyte death rate and macrophyte half-saturation (Figure 4).

4.2. Macrophyte Simulated and Observed Time Series

The simulated ensemble mean daily macrophyte biomass, shown in Figure 5, was obtained by considering only those parameter sets known to produce behaviors. The 769 parameter sets that produced behaviors were run through the model

Table 5. Correlations Between Model Parameter Values that Give Rise to Behaviors^a

Parameter	Description	Parameter	Description	Correlation Coefficient
c_{10}	macrophyte growth rate	c_{11}	macrophyte half saturation	0.73
c_4	epiphyte growth rate	c_{16}	epiphyte death rate	0.45
c_4	epiphyte growth rate	c_5	epiphyte half saturation	0.34
c_5	epiphyte half saturation	c_{16}	epiphyte death rate	-0.31
c_{11}	macrophyte half saturation	c_{12}	macrophyte self-shading	0.27

^aAll other correlations are greater than -0.11 and less than 0.16.

to produce 769 time series of macrophyte growth. Estimates of the mean, median, and standard deviations for each day in the time series were then calculated.

The observed biomass estimates were mean monthly values, except at Mildenhall where the values were estimated on a particular day. The observed mean monthly values are plotted in succession to create a 2-year-long time series (except those data for Mildenhall that represent 2 continuous years of sampling) for comparison with the simulated data. The observed data range from 0 to 35 g C m⁻² during January and February to peaks of between 65 and 135 g C m⁻² from late June to October. This reflects the physical differences between sites, which will include flow, climatic, and shading variations. The simulated data reproduce this generalized behavior, except during the winter months when the simulated biomass is lower than that observed. Most of the observed biomass estimates for nonwinter months, however, fall within the 1 standard deviation of the simulated mean time series except at Mildenhall.

4.3. Median Macrophyte and Epiphyte Time Series

Figure 6 shows the ensemble median behavior of the macrophytes and epiphytes (calculated from the 769 behavior sets) over the simulation period. The simulated macrophyte time series shows that on average, growth begins around day 74 (March 15, 1998) and reaches a peak of ~80 g C m⁻² on day 222 (August 10, 1998) and again in year 2 at around 80 g C m⁻² on day 593 (August 16, 1999). The simulated epiphytic growth causes the macrophyte growth to peak as any subsequent ep-

iphyte growth causes decay in the macrophyte biomass. The simulated epiphyte biomass peaks at around 2 g C m⁻² in both the first and second years. The peaks occur on day 280 (October 7, 1998) and day 664 (October 26, 1999), respectively. Observations of algal growth in the reach suggest a biomass peak during early summer [Jarvie *et al.*, 2001b], and as such, the simulated peak is later. However, the model does not simulate phytoplankton or epilyminic growth, which may explain this difference. When the epiphytes peak, the macrophyte biomass is close to zero. At this point the simulated epiphyte biomass declines also as the epiphytes are washed from the river reach.

4.4. Low and High Macrophyte Biomass Peaks

Of the 769 behaviors, 123 had peaks of between 50 and 75 g C m⁻², and 597 had peaks of between 75 and 150 g C m⁻² in both years, indicating the sensitivity of the model to different behavior criteria. As an indication of the factors controlling the occurrence of low and high biomass, a GSA was done using the two sets of behaviors, and the most significant parameters are listed in Table 6. The most important factor was self-shading. This parameter is a measure of the biomass at which growth is half the maximum. As such, the high values of the parameter cause high peak biomasses. The exchange of SRP between the pore water and the water column is important, as the macrophyte and epiphyte growth depends upon the SRP in the water column and pore water, respectively (equations (6) and (13)). Macrophyte growth has a value of 0.108 and as such is not significant even at the 90% level (0.121). Again, macrophyte

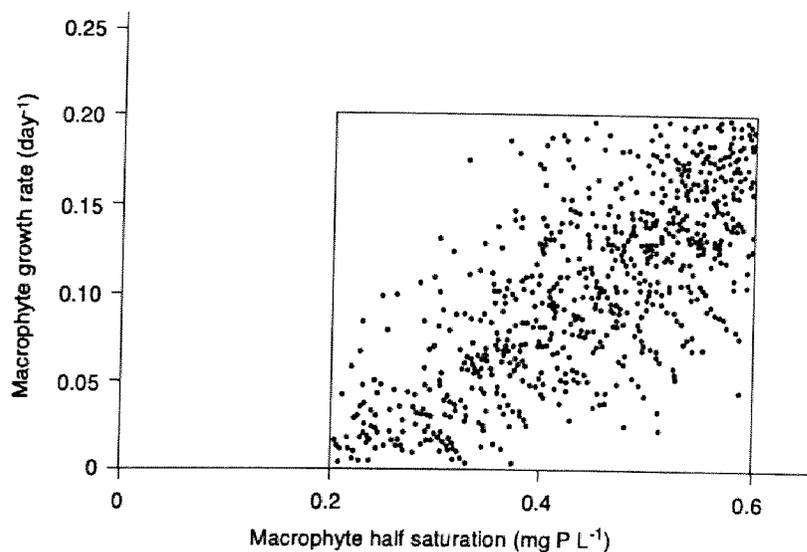


Figure 4. Relationship between macrophyte half saturation and macrophyte death rate to produce model behaviors. The correlation coefficient is 0.73. The box shows the range of values occupied by the nonbehaviors.

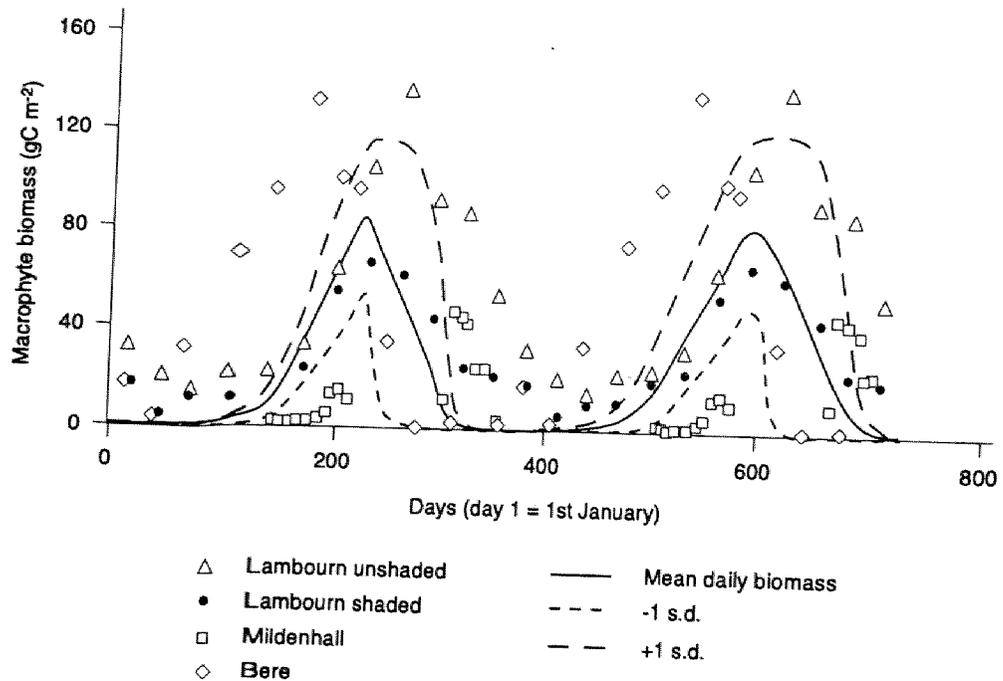


Figure 5. Simulated and observed mean daily macrophyte biomass. The mean daily biomass is estimated from the 769 result sets that produced behaviors. The observed data are mean monthly biomass estimates plotted against the midpoint of each month, expected at Mildenhall, which are daily values. The lines around the simulated means are ± 1 standard deviation.

death rate, which is flow related, was not important because the behavior criteria did not include any description of the minimum biomass, or when it should occur. The epiphyte death rate is important because it controls the epiphyte biomass, which is a control on the macrophyte growth.

4.5. P Behaviors

Of 10,000 simulations, 9831 parameter sets produced simulated output that fits the phosphorus behavior criteria (criteria 3–5) alone. Because of the low number of nonbehaviors the separations between the cumulative frequency curves are large,

thereby causing large values of the $K-S d_{m,n}$ statistic (Table 7). The most important parameters are those linked with the storage of TP in the streambed (the bulk sediment and pore water depths) and the exchange of SRP between the pore water and the overlying water column. The factors controlling the macrophyte and epiphyte dynamics are still important as they affect the uptake and release of SRP from the pore water and water column. In general, the parameter values that give rise to the nonbehaviors are grouped at the extremes of the parameter ranges. For the behaviors the parameter values are spread throughout the ranges.

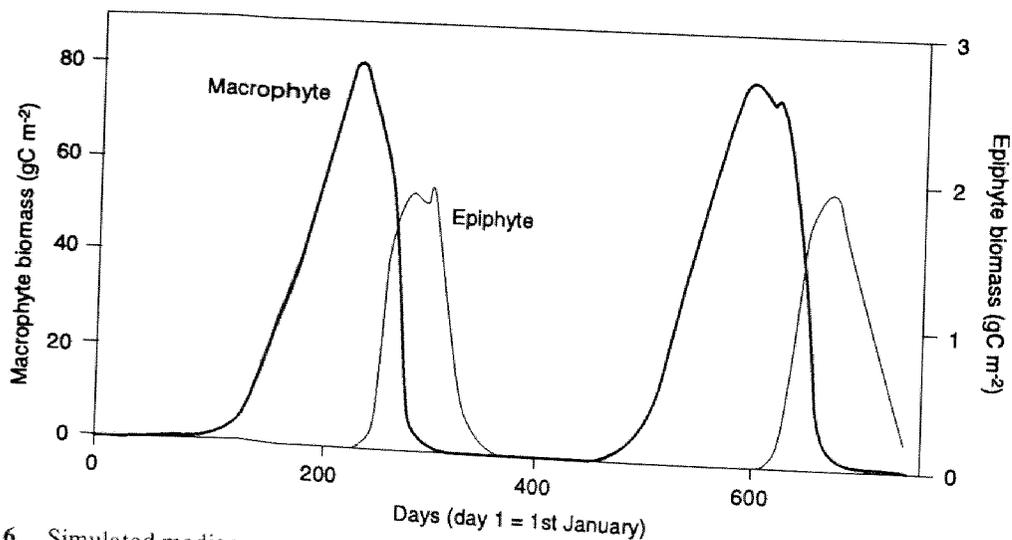


Figure 6. Simulated median macrophyte and epiphyte biomass. The median daily biomass is estimated from the 769 result sets that produced behaviors.

Table 6. Low and High Macrophyte Biomass^a

Parameter	Description	$d_{m,n}$
c_{12}	macrophyte self-shading	0.346
c_{16}	epiphyte death rate	0.284
c_4	epiphyte growth rate	0.244
c_5	epiphyte half saturation	0.220
c_{11}	macrophyte half saturation	0.192
c_7	P exchange	0.149

^aModel parameters significant at 95% level (0.135) or greater.

Plots of both the simulated ensemble mean TP and SRP concentrations show that the lines describing standard deviation virtually superimpose the mean concentration (Figures 7a and 7b). This indicates that the predominant influence on the output TP and SRP concentrations from the reach are the upstream inputs, rather than the internal processes in the reach. Figure 7 also shows that in comparison to the observed data the model is able to simulate the general dynamics of the TP and SRP concentrations.

5. Discussion

The "Kennet model" is one of the first models to simulate both P and macrophyte dynamics in a river system. This discussion focuses on the results of testing the model against generalized behavior criteria and suggestions are made regarding the work necessary to further test and improve the model. The fit of the simulated SRP and TP concentrations and the macrophyte biomass to observed data suggests that the mathematical representation of the system is reasonable as a first approximation. However, the system studied was not sufficiently dynamic with respect to P to allow complete testing of the internal process representations used in the model. Thus further applications of the model are required to data sets incorporating significant variations in the in-stream P dynamics, to test both the representation of the in-stream P dynamics and to give further credence to the ideas of Ham *et al.* [1981] regarding the factors controlling macrophyte behavior. Given the lack of P dynamics in the system studied, it was not possible to determine if the exact forms of the equations were ideal. Such determination is likely to be achieved only through more process-based studies, which will form mathematical relationships from data gathered in the laboratory or in the field and/or the derivation of mathematical expressions from first principles.

The GSA results indicate that 10 of the 14 parameters were shown to be sensitive in at least one of the evaluations. Thus

Table 7. Phosphorus^a

Parameter	Description	$d_{m,n}$
c_{13}	bed (bulk) sediment depth	0.711
c_7	P exchange	0.565
c_{11}	macrophyte half saturation	0.381
c_4	epiphyte growth rate	0.320
c_{10}	macrophyte growth rate	0.233
c_{12}	macrophyte self-shading	0.191
c_2	pore water depth (multiplier)	0.182
c_5	epiphyte half saturation	0.170
c_{16}	epiphyte death rate	0.141

^aModel parameters significant at 95% level (0.106) or greater.

nearly all the parameters, and by inference the processes that they relate to, are potentially important, which indicates that the model probably includes all the main processes necessary to simulate the P and macrophyte dynamics within the reach. Moreover, the GSA supports the idea that epiphytic algae can have a detrimental effect on *Ranunculus* growth by shading the macrophyte's leaves. When matching the behavior criteria (criteria 1-5), besides the parameters that relate to the macrophyte and epiphyte growth and death (Table 4), the model simulations suggest that the depth of the bed sediment is important, as is the sorption of P onto suspended sediment. The depth of the bed sediment will determine the amount of P available for uptake by the macrophytes, while a low sorption onto suspended sediment will generate more SRP in the water column that will then be available for epiphyte uptake. However, further application of the model is required to other systems showing a change in the P dynamics to more reliably isolate the key features of the interaction between P, macrophytes, and epiphytes.

Bulk sediment depth was the most important parameter when the model results were tested only against the P criteria (criteria 3-5), since again it determined the amount of P stored. Also in this case, the exchange of SRP between the pore water and overlying water column was important, given that it determines the relative amount of P in the water column and pore water and therefore the P available for macrophyte and epiphyte growth. The occurrence of nonbehavior arose with values of the bulk sediment depth at the extreme low end of the range. These low values corresponded to simulated SRP pore water concentrations that were too low. Given that values of P exchange are away from the extremes of the range, then this result indicates a net transfer of the pore water SRP into the overlying water column. In turn, this suggests that a shallow sediment layer (~10 cm), or the top layer of stratified sediment, may release SRP into the overlying water column. Unfortunately, these results offer no explanation as to the time-scale of release and no indication if the sediment may also scavenge SRP from the water column following the release. As such, further work is needed to assess if P is released from the streambed following a reduction in the P concentration of the overlying water column. Despite the influence of extreme parameter values on the behavior of the model, in general the model is not sensitive to the parameter values when only the P behavior criteria are considered. This suggests that the model output is being driven mainly by the upstream input rather than by any in-stream processes that are represented by the model. This is an important result because it suggests that the most important source of P to the reach is external. For other reaches in the Kennet river system this result may be different. A multireach model is required to investigate the influence of P transport and P release from sediments along the full length of the river.

The codependence of the macrophyte half saturation and growth rate is the major correlation identified between any of the model parameters. To obtain behaviors, when the half saturation is low, then the growth rate needs to be low also, and if the half saturation is high, then the growth rate needs to be high. This codependence arises because these two parameters are both multiplying factors in the same term of (17). The other correlations between the parameters generally are low, indicating that this bivariate analysis will add few insights into the model behavior not afforded by the K-S statistic. The possibility of parameter covariance (bivariate or multivariate)

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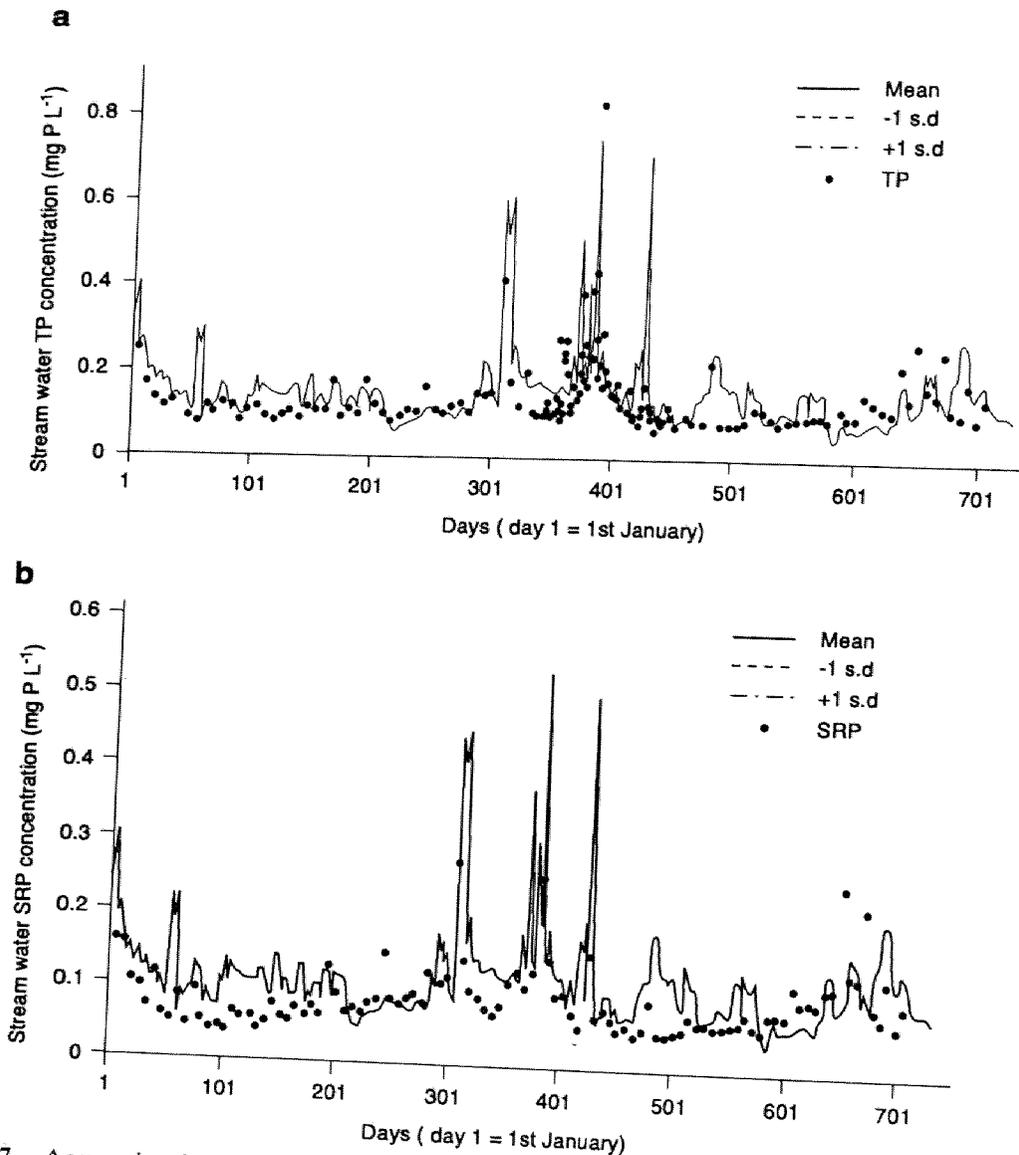


Figure 7. Accumulated mean simulated and observed (a) TP and (b) SRP concentrations. The mean daily concentrations are estimated from the 9831 results that produced behaviors. The mean value superimposes the lines that represent ± 1 standard deviation, indicating very low variation in model output between parameter sets which met the behavior criteria.

hiding important aggregate behavior-giving effects is uncertain and remains an important research area.

The model only accounts for the growth of epiphytes on the macrophyte biomass and does not simulate phytoplankton or epiphytic growth in the reach. As such, the model output does not simulate the peak in algal biomass observed in spring by *Jarvie et al.* [2001b]. The model equation describing epiphyte growth is based on a Lotka-Volterra predator-prey relationship (equation (18)). Thus the simulated epiphyte biomass will always peak after the onset of macrophyte growth because the epiphytes can only grow in the presence of macrophytes. To simulate phytoplankton and epiphytic algal growth independent of macrophytes, equations will need to be added to the model. Such equations are likely to be a function of flow, SRP availability, solar radiation, water temperature, and macrophyte biomass and may take the form of those used to model algal growth in the River Thames by *Whitehead and Hornberger* [1984].

While the model could be used to simulate environmental

changes over a long time period in response to time series inputs, there would be a question over the results because the parameter values would be constant for the model run. In reality it may be expected that the process interactions that the parameters represent will change with time. As such, while this remains a major challenge, it may be possible to use the model to simulate the steady state conditions before and after the environmental perturbation. To address these issues, future work must include application of the model to specific case studies of environmental change where data describing the change are available. Moreover, different behavior criteria may be defined, so that the model could be used to investigate which parameters are important under different physical conditions. For example, given a change in the flow inputs, a GSA could be done to see what parameters controlled a low or high macrophyte biomass. For some purposes, the model may need to be linked to models of C and N to develop a fully integrated picture of nutrient uptake. More detailed investigations of

changes in P loads also could be constructed. Such scenarios would correspond to a change in the input from the STW, a particularly relevant topic given the current implementation of the Urban Waste Water Directive and the impacts of changed flow conditions.

The Monte Carlo results have also identified a generalized set of model parameter ranges, which are drawn from observations reported in the literature. Following successive Monte Carlo trials, these parameter ranges could be narrowed to give a set of parameters specific to a particular case study [Spear and Hornberger, 1980]. However, running the model with altered inputs in a Monte Carlo framework allows for the uncertainty in the model parameters. The model was able to simulate the generalized macrophyte growth pattern observed in some rivers draining Chalk catchments in southern England; however, to test the structural uncertainty in the model, it is necessary to apply it to other sites to gain some indication of the transferability both of its structure and generalized parameter set. The parameter ranges used in the Monte Carlo simulations affect the number of behaviors achieved given a set number of model runs, as do the definitions of the system behavior. As such, it is expected that the interaction of the parameter ranges and the systems definitions will influence the standard deviations of the simulated output (e.g., Figures 7a and 7b). Studying such interactions and the influence on the model output is an issue requiring further research.

Despite the need for further model applications to fully test the internal process representations and the problems of structural and parameter uncertainty, this study's findings have demonstrated the model's utility. Namely, the model provides a basis for formalizing the concepts regarding the in-stream processes and thereby allows for hypothesis testing regarding process interaction. Furthermore, the model can be used as a learning tool for examining the dynamics of water quality change in response to altered flow or P inputs, an important attribute given the need to improve the understanding of river system functioning for scientific and management purposes.

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