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On modelling the flow controls on macrophyte and epiphyte dynamics in a lowland permeable catchment: the River Kennet, southern England

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Abstract

A new in-stream model of phosphorus (P) and macrophyte dynamics, the Kennet Model, was applied to a reach of the River Kennet to investigate the impacts of changing flow conditions on macrophyte growth. The investigation was based on the assessment of two flow change scenarios, which both included the simulation of decreasing total phosphorus concentrations from a sewage treatment works due to improved effluent treatment. In the first scenario, the precipitation and potential evaporation outputs from a climate change model (HadCM2 GGx) where input into the catchment model INCA to predict the mean daily flows in the reach. In the second scenario, the mean daily flows observed in a historically dry year were repeated as input to the in-stream model to simulate an extended low flow period over 2 years. The simulation results suggest that changes in the seasonal distribution of flow were not detrimental to macrophyte growth. However, the simulation of extended periods of low flow suggests that a proliferation of epiphytic algae occurs, even when the in-stream phosphorus concentrations are reduced due to effluent treatment. This epiphytic growth was predicted to reduce the macrophyte peak biomass within the reach by approximately 80%. Thus, the model simulations suggest that flow was more important in controlling the macrophyte biomass in the River Kennet, than the in-stream phosphorus concentrations, which are elevated due to agricultural diffuse sources.

Keywords: Basin management; Rivers; Water quality; Kennet model; INCA; Mathematical model; Climate change; Phosphorus; Soluble reactive phosphorus; Macrophytes; Epiphytes; River Kennet

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1. Introduction

Macrophyte growth is dependent on a range of environmental and biological factors including nutrient availability, flow, turbulence, solar radiation, water temperature, sediment depth and epiphytic growth (Ham et al., 1981). Perturbations in these factors determine the relative abundance of different macrophyte species and therefore, it is important to identify the potential impacts of likely perturbations in these controlling factors on the plant community, particularly if the community includes a rare or highly valued genus or species. For example, *Ranunculus* is important in the Chalk streams of southern England because the plant provides a habitat for invertebrates and fish. Furthermore, given the distribution of such a species can influence the utilisation of the water resource in terms of effluent discharge, abstraction and recreational activities then for resource management it is important to understand how the system functions.

Phosphorus (P) is now recognised as the major limiting nutrient in UK freshwater systems, and as such is probably the key nutrient in determining macrophyte growth. The main sources of P to lakes and river systems are from diffuse agricultural sources and from sewage treatment works (STW) and industrial point sources (Jarvie et al., 1998). Nutrient enrichment resulting from these sources is a growing problem in many UK lowland rivers, especially during the summer when there is less water available to dilute the sewage inputs. The balance between sewage inputs and river flow is subject to change in the UK lowlands due to increasing urbanisation, groundwater abstraction and projected patterns of climate variability leading to higher evapotranspiration and correspondingly more extreme low-flow conditions (CCIRG, 1991; Hulme and Jenkins, 1998). Low flow conditions can encourage epiphytic algal growth and under such conditions, the epiphytes, and the detritus that they trap, can form a thick layer that shades the macrophyte's surface, thus restricting the macrophyte's rate of photosynthesis (Sand-Jensen, 1977; Phillips et al., 1978). Given the potential adverse impacts on river ecology due to P enrichment and reduced flows, it is important to understand and quantify how changes in P availability, flow and epiphyte growth will affect macrophyte growth. However, developing strategies to control the impacts of phosphorus on the aquatic ecology is difficult because phosphorus in aquatic environments is highly dynamic, with phosphorus cycling between the water column, the sediments and the biota (Mainstone et al., 2000). Furthermore, the effects of the controlling factors on macrophyte growth are an integrated result, and as such it is difficult to determine the affect of an individual factor. To this end, mathematical models are useful as they serve as an aid to understanding complex systems and, moreover, they begin to quantify future changes under likely scenarios.

A new mathematical model of in-stream P and macrophyte dynamics, the Kennet Model, has been recently developed and applied to a reach of the River Kennet (Wade et al., 2002a,b). The River Kennet provides an important case study for two reasons. Firstly, the Kennet drains a catchment underlain mainly by a Cretaceous Chalk aquifer that is typical of large areas of lowland UK, and secondly, P has been removed from the effluent of a STW located in the river's upper reaches. The objective of the work presented is to apply the model to explore how the physical and chemical factors control macrophyte and epiphyte growth. Thus, whilst it is recognised that biological factors such as species competition will also affect the macrophyte growth, these factors are not considered in this case. Specifically, the work presented aims to assess how macrophyte biomass responds to: (a) a flow change scenario generated by a climate change model; and (b) the simulation of a 2-year low flow period. With respect to each aim, the response will be assessed against a background of high (pre-P removal) and low (post-P removal) P inputs from the STW.

2. Study area, sampling and analysis

The River Kennet (approx. 1100 km^2) drains a Cretaceous Chalk catchment in southern England (Fig. 1). Rising from a source at 190 m, the river

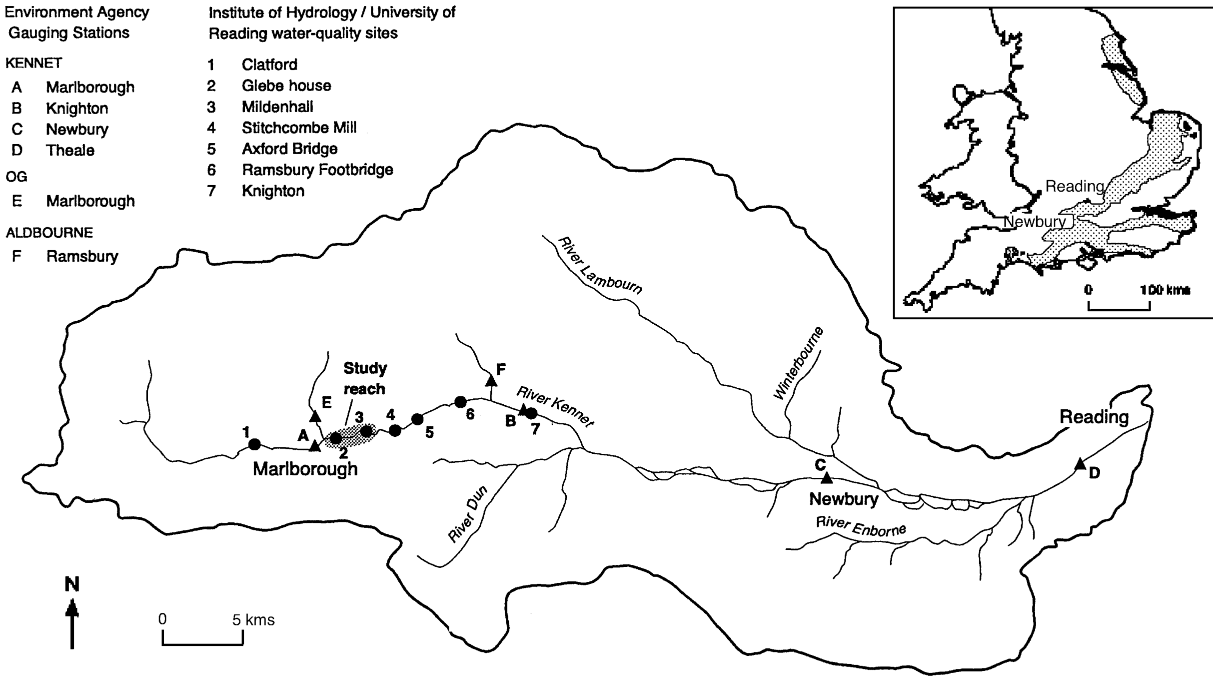

Fig. 1. Schematic of the River Kennet Catchment. The inset shows the location of Cretaceous Chalk within England.

flows broadly eastwards for approx. 40 km before entering the River Thames at Reading. The Cretaceous Chalk is fairly ubiquitous within the catchment and covers approximately 80% of the total area. Gently sloping valleys dominate the relief and the altitude ranges from 32 m at the confluence with the Thames, to 294 m at the highest point on the Marlborough Downs. The Kennet has five major tributaries: the Lambourn; the Enbourne; the Dun; the Og; and the Aldbourne.

The hydrology of the Kennet catchment, taken from NERC (1998) is, in brief, as follows. The long-term annual precipitation over the catchment is 774 mm, though approximately only 38% becomes river flow due to high evapotranspiration. Much of the precipitation is percolated into the Chalk aquifer, and consequently the flow response is highly damped, except in the clay-lined River Enbourne tributary. The long-term annual mean flow at Theale, the lowest gauging station on the Kennet is 9.5 m^3 s^{-1} (or 291 mm of runoff), and the Q10 and the Q95 flows are estimated as 16.7 and 3.7 m^3 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 is 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 day^{-1} is abstracted from the chalk aquifer by 33 boreholes arranged in seven well fields that make up the West Berkshire groundwater scheme.

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). In this study, the model is applied to a reach that lies 1.5-km downstream of Marlborough gauging station, and is itself 1.5-km long from site 2 to site 3 (Fig. 1), Marlborough STW discharges immediately upstream of the reach. Weekly water chemistry samples were taken upstream of the reach and the STW at Clatford (site 1), and from the downstream end of the reach at Mildenhall (site 3) from June 1997 to December 1999. These samples were analysed for total phosphorus (TP), soluble reactive phosphorus (SRP), boron (B) and suspended sediment concentrations amongst other determinands (Jarvie et al., 2002a). Thames Water provided mean daily flows and TP concentrations relating to the effluent discharged from Marlborough STW. An automatic weather station (AWS) was located alongside the reach providing daily solar radiation data, and a Hydrolab continuous monitor was also installed thereby providing daily water temperature data. The macrophyte and epiphyte biomass within the reach was measured when practical between April 1998 and December 1999 (Flynn et al., 2002). The epiphyte biomass measured provides an estimate of the algal growth on the macrophytes. The flows in the reach were calculated by mass balance from the daily measurements recorded at the Environment Agency gauges located on the Kennet at Marlborough and Knighton, the Og at Marlborough and the Aldbourne at Ramsbury (Wade et al., 2002a).

3. Methods

3.1. Kennet model description

The Kennet model is described in detail elsewhere (Wade et al., 2002a,b). Briefly, the model is a mathematical representation of the major stores in the aquatic P cycle, and the in-stream processes that determine the transfer of P between those stores (Fig. 2).

At present the model, which is dynamic and operates on a daily time step, is designed to simulate a single reach. As such, it simulates the mean daily flow, SRP, TP, boron and suspended sediment streamwater concentrations in the water column, and the SRP concentrations in the pore water and the TP associated with the bed sediments (Table 1). In addition, the model also simulates the resuspension of bed sediment, the deposition of suspended sediment 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 the water column SRP and TP concentrations. Inputs to the model include measured and estimated time series data describing the flow, sediment and TP concentrations into the reach (Table 2). Streamwater 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, useful for mass balance, whilst SRP is a measure of the dissolved P in the streamwater which is biologically available. Furthermore, measured SRP and TP concentrations are available for a site upstream (Fig. 1, site 1) of the STW input, at the end of the Mildenhall reach and 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 (also known as DHP, dissolved hydrolysable phosphorus). In this study, the total macrophyte biomass is defined as including all submerged and emergent species, given all macrophytes will influence the total phosphorus available. 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 (Table 3). The rates of mass transfer between stores are modelled as first-order (linear) exchanges and these rates are represented as parameters in the equations (Table 4).

3.2. Model calibration

The model was initially calibrated to the observed mean daily flow, weekly TP and SRP concentrations and the weekly macrophyte and epiphyte data. For model calibration the period simulated was from 1 January 1997 to 31 December 1998. This period was chosen because all the necessary input data were readily available and, moreover, the period covers times before, during and after effluent treatment at Marlborough STW where effluent treatment began in September 1997. Determining a unique set of model parameters through calibration is difficult because of structural uncertainty in the model, and the prob-

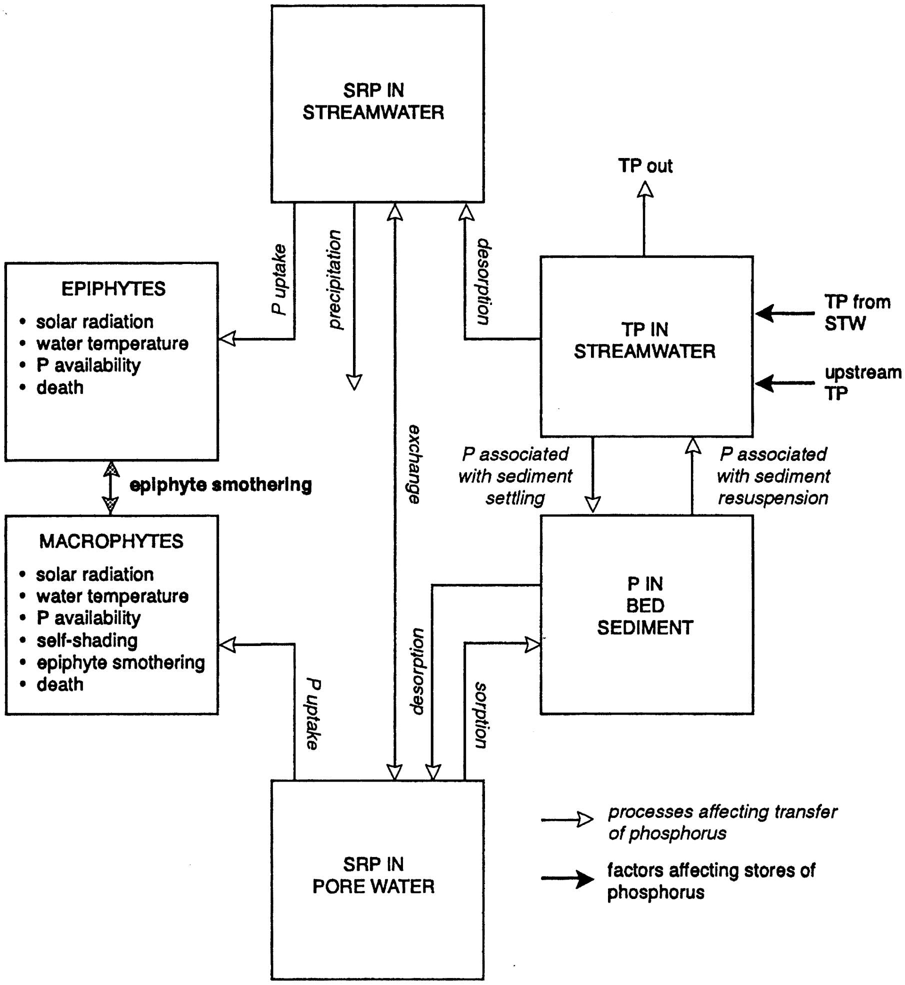

Fig. 2. Schematic of the model of in-stream phosphorus dynamics showing the main stores and transfer processes. The model is described in detail in Wade et al. (2002a).

lems associated with scaling field data in both space and time to provide appropriate parameter values (Oreskes et al., 1994; Neal et al., 2002). Given this, model calibration was achieved using a Monte Carlo technique. Namely, the model was run 10 000 times and the output compared against a set of pre-defined behaviour criteria. These criteria and the model set-up are identical to that described in Wade et al. (2002b) and are summarised in Table 5. On each run, parameter values where chosen randomly from specified ranges determined from the literature. Each parameter set that generated a model output that fitted the behaviour criteria was kept, and subsequently used for the model scenario runs. Of the 10 000 runs, 277 parameter sets that produced model output that matched the behaviour criteria were identified. Since the model is dependent upon initial conditions then the first 30 days of model output where not used in the calculation of any statistics used to check the model output with the behaviour criteria. During this initial period it is assumed that the dependency of the model output on the initial conditions shifts to a dependency on the input time series. This assumption seems reasonable for three reasons. Firstly, the

Table 1
Model outputs

Variable	Description	Units
x_1	Flow out of reach at time, *t*	$m^3\ s^{-1}$
x_2	Suspended sediment at time, *t*	$mg\ l^{-1}$
x_3	Moveable bed load at time, *t*	$kg\ m^{-2}$
x_4	TP in water column at time, *t*	$mg\ P\ l^{-1}$
x_5	B in water column at time, *t*	$g\ P\ m^{-2}$
x_6	TP in pore water at time, *t*	$mg\ P\ l^{-1}$
x_7	Macrophyte biomass at time, *t*	$g\ C\ m^{-2}$
x_8	Epiphyte biomass at time, *t*	$g\ C\ m^{-2}$
x_9	Grain diameter suspended at time, *t*	μm
x_{10}	Concentration of sediment resuspended or settled at time, *t*	$mg\ l^{-1}$
x_{11}	SRP in water column at time, *t*	$mg\ P\ l^{-1}$
x_{12}	SRP in pore water at time, *t*	$mg\ P\ l^{-1}$
T_1	Residence time of water in reach at time, *t*	day
VEL	Water velocity in reach at time, *t*	$m^3\ s^{-1}$

initial conditions relating to flow, TP concentration and the macrophyte and epiphyte biomass are derived from observed data. Secondly, observed daily flow and weekly TP concentration time series are used as input data. Thirdly, previous simulations show that the output flow, suspended sediment, SRP and TP concentrations from the first day of the simulation match to a reasonable degree of accuracy those observed (Wade et al., 2002b).

Table 2
Input time series and constants

Input variable Time series	Description	Units	Measured/ Estimated
u_1	Flow into reach at time, *t*	$m^3\ s^{-1}$	E^a
u_2	Suspended sediment at time, *t*	$mg\ Sed\ l^{-1}$	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*	$m^3\ s^{-1}$	M
u_6	TP concentration in sewage effluent at time, *t*	$mg\ P\ l^{-1}$	M
R	Solar radiation at time, *t*	Normalised 0–1[c]	M
T	Water temperature at time, *t*	°C	M
u_9	Lateral flow into reach at time, *t*	$m^3\ s^{-1}$	E^a
u_{10}	B concentration in sewage effluent at time, *t*	$mg\ B\ l^{-1}$	E^b
Constants			
L	Reach length	m	M
w	Reach width	m	M
PM	Change in potentially moveable bed mass with respect to grain diameter	$kg\ \mu m^{-1}$	M
B_{in}	Total *B* concentration from all sources into reach at time, *t*	$mg\ B\ l^{-1}$	E
P_{in}	Total TP concentration from all sources into reach at time, *t*	$mg\ P\ l^{-1}$	E

Abbreviations: M = measured data available for input; E^a = flows estimated from measurements at nearest gauging stations; E^b = *B* effluent input estimated from mass-balance within reach. [c]The original time series of net radiation values ($W\ m^{-2}$) were normalised to the range 0 to 1 by dividing by the maximum value observed.

Table 3
The model equations

Determinand	Equation
Flow	$\frac{dx_1}{dt} = \frac{(u_1 + u_5 + u_9 - x_1)}{T_1}$
Suspended sediment	$\frac{dx_2}{dt} = \frac{(u_2 - x_2)}{T_1} + \frac{1000}{V}(\frac{dPM}{dx_9})(\frac{dx_9}{dt})$
	$= \frac{(u_2 - x_2)}{T_1} + \frac{dx_{10}}{dt}$
Bed mass moved	$\frac{dx_3}{dt} = \frac{1}{Lw}(\frac{dPM}{dx_9})\frac{dx_9}{dt}$
Water column TP	$\frac{dx_4}{dt} = \frac{(P_{in} - x_4)}{T_1} - \frac{c_3 c_4 x_8 x_7 R x_{11} \theta_E^{(T-20)} wa}{(u_1 + u_5 + u_9)^{1-b}(c_5 + x_{11})}$
	$+ c_7(x_{12} - x_{11}) - c_8 x_{11} + \{\begin{matrix}\text{gain}\\ \text{loss}\end{matrix}\}$
	$P_{in} = \frac{(u_4 u_1 + u_6 u_5 + 0.016 u_9)}{(u_1 + u_5 + u_9)}$
	$+ \frac{1}{\rho_s(1-n)} x_6 \frac{dx_{10}}{dt} 10^{-3}$ gain
	$+ K_D^{Sus} x_{11} \frac{dx_{10}}{dt} 10^{-6}$ loss
Boron	$\frac{dx_5}{dt} = \frac{B_{in} - x_5}{T_1}$
	$B_{in} = \frac{(u_1 u_3 + u_5 u_{10})}{u_1 + u_5 + u_9}$
TP associated with the bed sediment	$\frac{dx_6}{dt} = -\{\begin{matrix}\text{gain}\\ \text{loss}\end{matrix}\} - c_7(x_{12} - x_{11})n$
	$- \frac{c_{15} c_{10} \theta_M^{(T-20)} x_7 x_{12} R c_{12}}{p(c_{11} + x_{12})(c_{12} + x_7)} n$
	$+ 10^{-6} x_{11} K_S^{Sus} \frac{dx_{10}}{dt} \frac{(u_1 + u_5 + u_9)^{1-b}}{wa} \frac{1}{c_{13}}$ gain
	$+ 10^{-3} x_6 \frac{1}{\rho_s(1-n)} \frac{dx_{10}}{dt} \frac{(u_1 + u_5 + u_9)^{1-b}}{wa} \frac{1}{c_{13}}$
loss	
Macrophyte biomass	$\frac{dx_7}{dt} = \frac{c_{10} \theta_M^{(T-20)} x_7 x_{12} R c_{12}}{(c_{11} + x_{12})(c_{12} + x_7)} - c_{14} x_7 x_8 x_1$
Epiphyte biomass	$\frac{dx_8}{dt} = \frac{c_4 \theta_E^{(T-20)} x_8 x_7 R x_{11}}{(c_5 + x_{11})} - c_{16} x_8 x_1$
Mean grain diameter	$\frac{dx_9}{dt} = c_1(\frac{u_1 + u_5 + u_9 - x_1}{T_1})$
Sediment resuspended or deposited	$\frac{dx_{10}}{dt} = \frac{1000}{V} \frac{dPM}{dx_9} \frac{dx_9}{dt}$
Water column SRP	$x_{11} = \frac{0.75 \cdot x_4}{1 + (10^{-6} K_D^{Sus} x_2)}$
Pore water SRP	$x_{12} = \frac{0.75 \cdot x_6}{1 + \frac{K_D^{Bed}}{p} 10^{-3} x_3}$

Table 4
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	μm s m^{-3}	1–10	5–50	Estimated
c_2	Pore water depth (multiplier)	[∅]	0.25–0.45	0.25–0.45	Estimated
c_3	Proportion of P in epiphytes	g P g^{-1} C	0.0054	0.0054[a]	Dawson, 1976
c_4	Epiphyte growth rate	m^2 g C^{-1} day^{-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	dm^3 kg^{-1}	200	100–300	Jarvie et al., 2002a
c_7	P exchange (water column\ pore water)	day^{-1}	0.4–86.4	0.3–3.0	Wagner and Harvey, 1997
c_8	Precipitation of P in water column	day^{-1}	0.68	0.35–1.05	House et al., 1995
c_9	K_d for bed sediment, K_d^{Bed} (as a fraction of K_d^{sus})	[∅]	0.1 – 1.0	0.1–1.0	Jarvie et al., 2002a
c_{10}	Macrophyte growth rate	day^{-1}	0.1–0.8	0.2–0.6	Dawson, 1976 Wright et al., 1982
c_{11}	Half-saturation of P for macrophyte growth	mg P l^{-1}	0.0002–0.496	0.002–0.2	Bowie et al., 1985
c_{12}	Self-shading	g C m^{-2}	74	10–50	Dawson, 1976
c_{13}	Bed (bulk) sediment depth	m	0.1–1.0	0.1–1.0	Estimated
c_{14}	Macrophyte death rate	s g C^{-1} day^{-1}	0.01–0.3	0.01–1.0	Chapra, 1997
c_{15}	Proportion of P in macrophytes	g P g^{-1} C	0.0054	0.0054[a]	Dawson, 1976
c_{16}	Epiphyte death rate	s day$_3^{-1}$ m^{-}	0.01–0.05	0.01–0.05	Bowie et al., 1985
θ_M	Macrophyte temperature dependency	[∅]	1.01–1.066	1.066[a]	Bowie et al., 1985
θ_E	Epiphyte temperature dependency	[∅]	1.01–1.066	1.066[a]	Bowie et al., 1985
n	Porosity	[∅]	0.3	0.3[a]	Chow et al., 1988
ρ_s	Bulk sediment density	kg m^{-3}	2.65	2.65[a]	Chow et al., 1988
A	Velocity–flow parameter	m^{-2}	0.18	0.18	Estimated
B	Velocity–flow parameter	[∅]	0.68	0.68	Estimated

[a] Model parameters fixed with a single value for model simulations since literature suggested these were the most appropriate values. Estimated = parameter values estimated through calibration and expert knowledge.

Table 5
Model behaviours

Factor	Behaviour	Reference
Macrophyte biomass	Peak macrophyte biomass must be <100 g C m^{-2} in year 1 and >50 g C m^{-2} and l <150 g C m^{-2} in year 2 Peak macrophyte biomass must occur between 1 May and 1 August in year 1 and between 1 August and 1 October in year 2	Dawson, 1976 Wright et al., 1982 Flynn et al., 2002
Epiphyte biomass	The peak in the epiphyte biomass must occur between 1 May and 1 September in year 1 and between 1 August and 1 December in year 2	
Suspended sediment	Daily suspended sediment concentrations must be greater than 0.2 and less than 250 mg l^{-1}	Jarvie et al., 2002a
Pore water SRP	Mean annual pore water SRP concentrations must be greater than 0.1 and less than 10 mg P l^{-1}	Jarvie et al., 2002a
Water column SRP	Mean annual water column SRP concentrations must be less than 0.2 mg P l^{-1}	Jarvie et al., 2002a

3.3. Model scenarios

To investigate the potential impact of climate change and hence changing flow conditions on the P and macrophyte dynamics, two scenarios were investigated. The first scenario investigated the impact of altered flow seasonality caused by the spatial and temporal shifts in the global patterns of precipitation, evaporation and temperature. The second investigated the affects of a 2-year low flow period. In the subsequent sections of this paper the flow seasonality and extended low flow scenarios are referred to as scenario 1 and 2, respectively.

3.4. Seasonal flow patterns

To determine the impact of changes in flow seasonality, a new mean daily flow input time series was generated for 1997 and 1998. This was achieved by using forecasted changes in precipitation and potential evaporation derived from the Hadley Centre Coupled Model version 2 (HadCM2), a general circulation model (Johns et al., 1997) to scale precipitation data, and then by running the scaled precipitation through the INCA model (integrated nitrogen catchment model, Whitehead et al., 1998) to generate the new flow time series (Limbrick et al., 2000). The precipitation data was obtained from the Meteorological Office as a spatially weighted average for the Kennet catchment. This precipitation data was scaled by the forecasted percentage change in precipitation and then converted to hydrologically effective precipitation by using MORECS and the modelled potential evaporation derived from HadCM2 (Thompson et al., 1981; Hough et al., 1997; Table 6). An estimated soil moisture deficit time series was also derived. The HadCM2 model is a coupled ocean-atmosphere general circulation model (GCM) with a spatial resolution of 2.5° latitude × 3.75° longitude. The output from the model, which relates to a period approximately 2050, was disaggregated to 0.5° × 0.5° grid squares to provide data for the location of the Kennet catchment (Limbrick et al., 2000). The climate change simulations assumed that the forecast changes depended only upon future changes in greenhouse gas concentrations. The effects of sulfate aerosols on climate were not

Table 6
Forecast monthly changes in the rainfall, potential evaporation (PE) and temperature in the River Kennet catchment (after Limbrick et al., 2000)

Change in:	Jan.	Feb.	Mar.	Apr.	May.	Jun.
Rainfall (%)	9.5	14.0	4.4	7.5	2.0	−3.3
PE (%)	−19.6	−11.8	−1.1	1.8	3.7	2.1
Temperature (°C)	1.4	1.4	1.3	1.2	1.2	1.0
Change in:	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Rainfall (%)	−15.8	−9.0	1.1	5.6	14.6	14.9
PE (%)	7.9	15.4	17.1	8.0	−15.0	−30.0
Temperature (°C)	1.4	1.6	1.6	1.5	1.5	1.6

These changes were forecast using the Hadley centre's climate model (version 2, HadCMv2) that incorporated the effects of greenhouse gas forcing alone.

considered, as such impacts are highly uncertain at present (Hulme and Jenkins, 1998).

INCA was initially calibrated to the flow conditions observed in 1997 and 1998 using hydrologically effective precipitation data derived from spatially weighted precipitation and evaporation data collected by the Meteorological Office at their observation sites. The hydrologically effective precipitation and soil moisture deficit values derived from the climate scenario where then input into the INCA, and the new flow time series derived.

The fit of the simulated flow output, resultant from the initial calibration, to that observed was good at the gauging stations in the lower reaches of the catchment but in the upper reaches, the simulated flows tended to be an overestimate when compared to the observed flows, though the dynamics were reasonable (Table 7). In the upper Kennet it is known that the topological catchment area is greater than the hydrological catchment area (NERC, 1998). It is the topological catchment area that is used within INCA to generate the flow estimates, and therefore this seems a likely explanation for the over-estimation. To overcome this problem, the daily flow time series resultant from the scenario simulation was divided by the flow time series derived through the calibration of INCA. This produced a time series of ratios, which represent the changes in the mean daily flow pattern due to the climate change scenario. These ratios were then multiplied by the corresponding mean daily flows input to the in-stream P model during its calibration to give a new scenario input flow time series for use within the in-stream model.

Using these scenario flow data, the in-stream P model was run with the 277 parameter sets which where observed to give output values within specific behaviour criteria during the calibration phase (Wade et al., 2002b). Estimates of the median, 10 (Q10) and 90 (Q90) percentiles and standard deviations for the flows, SRP and TP concentrations and macrophyte and epiphyte biomass on each day in the time series were then calculated. The median was used rather than the mean because it is less affected by extreme values. The distribution of outputs around the mean is also skewed and therefore, the Q10 and Q90 giving a better indication of the spread of values rather than the standard deviation which assumes a normal distribution.

3.5. Two-year low-flow period

To assess the impact of the 2-year low-flow period, the 1998 input flow data used for model calibration were deleted from the input time series and replaced by the 1997 input flow data, as such, the 2-year time series represented two repetitions of the 1997 flows. These flows represent extreme low-flow conditions for the River Kennet. The flows observed in 1997 were very low, because of the lower than average precipitation throughout 1996 and during the winter of 1997. Again the 277 parameter sets that produced model

Table 7
Co-efficient of determination (as defined by Nash and Sutcliffe, 1970) relating INCA simulated mean daily flows to those observed

Site	Co-efficient of determination
Marlborough	0.66
Knighton	0.78
Newbury	0.77
Theale	0.63

behaviours during calibration were run through the in-stream model with the scenario mean daily flow data. Five of the parameter sets produced outputs where the solution of the equations representing the TP and SRP concentrations in both the water column and pore water became numerically unstable. As such, these model outputs were rejected from the subsequent analysis. Again estimates of the median and the 10 and 90 percentiles for the output flows, SRP and TP concentrations and macrophyte and epiphyte biomass on each day in the time series were calculated.

4. Results

4.1. Simulated flows

The median flow outputs resulting from calibration and scenarios 1 and 2 are shown in Fig. 3. Due to the wetter winters forecast by the HadCMv2 model then the flows relating to scenario 1 are generally higher in both years than the simulated flow generated during model calibration. Only in December (from day 324 to 366) in the first year do the scenario 1 flows fall below those in the calibration output flow time series. This result suggests that if the climate model is broadly representative of future climate changes then, in terms of the seasonal precipitation distribution, higher flows can be expected during the spring and summer. As such, the periods of higher flow will correspond to the periods of macrophyte and epiphyte growth in the Chalk rivers of southern England. However, this simple pattern may be perturbed by a succession of dry years. For the 2-year low-flow scenario, given the original flows in 1997 were repeated for the second simulation year then in the second year the flows for this scenario are lower than both the calibration and scenario 1 flows. The simulated flows for the first simulated year during calibration and in scenario 2 are below the Q95 flow (0.57 m^3 s^{-1}) estimated for Knighton gauging station 82% of the time.

4.2. Simulated SRP and TP concentrations

The SRP and TP concentrations simulated during model calibration and scenarios 1 and 2 change according to the amount of water available to dilute the inputs from the STW (Fig. 3b,c). Prior to effluent treatment (September, 1997), both the SRP and TP concentrations are lowest for scenario 1 because more water is available to dilute the P inputs from the STW. After effluent treatment the lowest amount of water is available for dilution occurs in scenario 2, and therefore, both the SRP and TP concentrations are higher in year 2 for this scenario than during calibration or scenario 1.

4.3. Simulated macrophyte and epiphyte biomass

In the first year the simulated macrophyte peak biomass is very similar in all three cases at approximately 40 g C m^{-2}, though the biomass in scenario 1 has a slightly higher peak that occurs a few days later than for the model calibration and scenario 2 (Fig. 3d). In the second year, the peak biomasses are 77, 43 and 15 g C m^{-2} for model calibration and scenario 1 and 2, respectively. The timing of the peak obtained during calibration in mid-August is also approximately 100 days later than in the other two cases, where the two peaks in macrophyte biomass coincide. For the calibration and scenario 2 cases the onset of macrophyte growth occurs at the same time (approx. day 480) whereas for scenario 1 the onset of growth occurs earlier, approximately day 385. This earlier growth

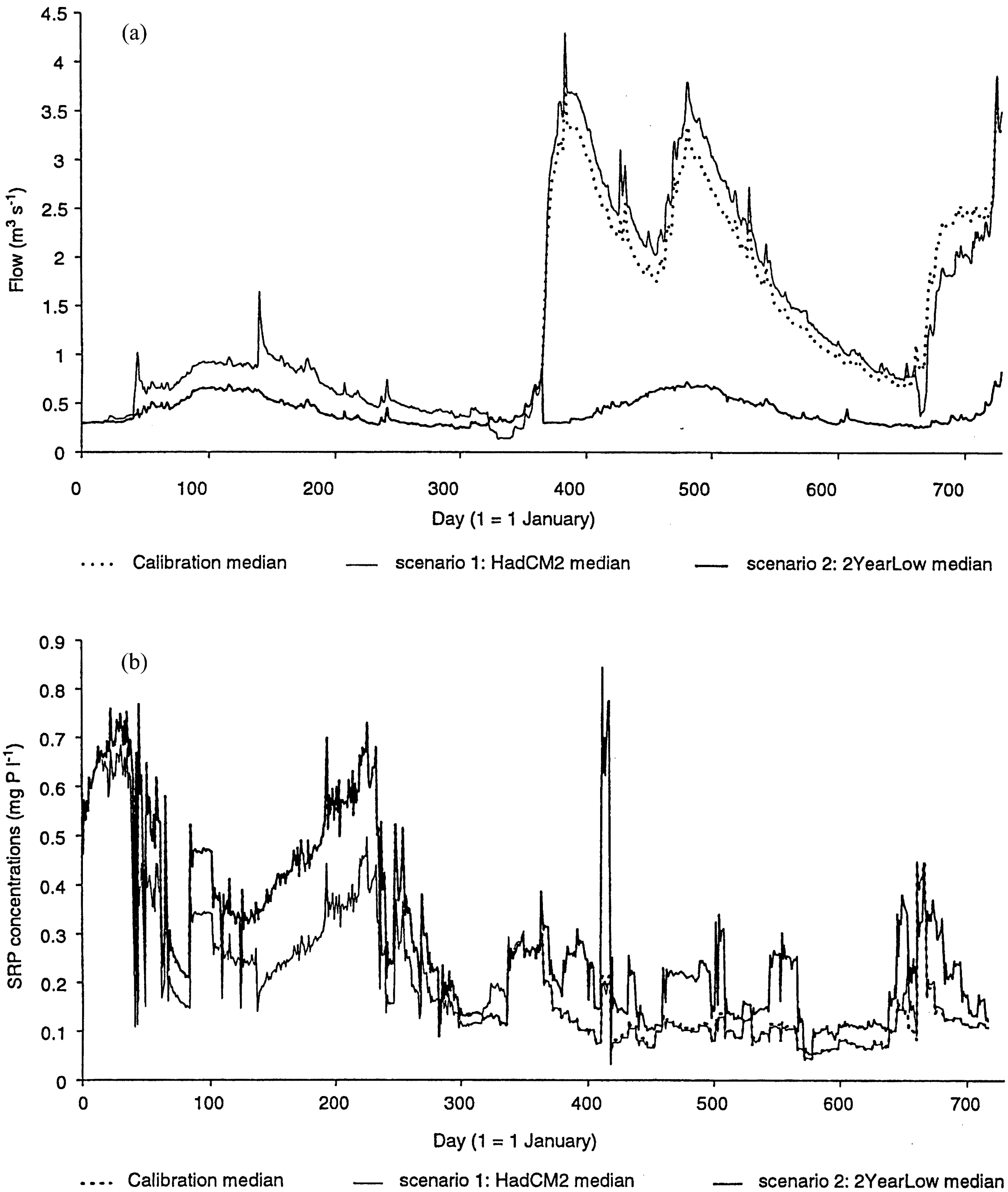

Fig. 3. (a) The original flows calculated from the mass-balance of observed flows in 1997 and 1998 and the flows generated for the HadCM2 and extended low flow scenarios and the affects of the different flow conditions on the (b) SRP and (c) TP concentrations and the (d) macrophyte and (e) epiphyte biomass estimates.

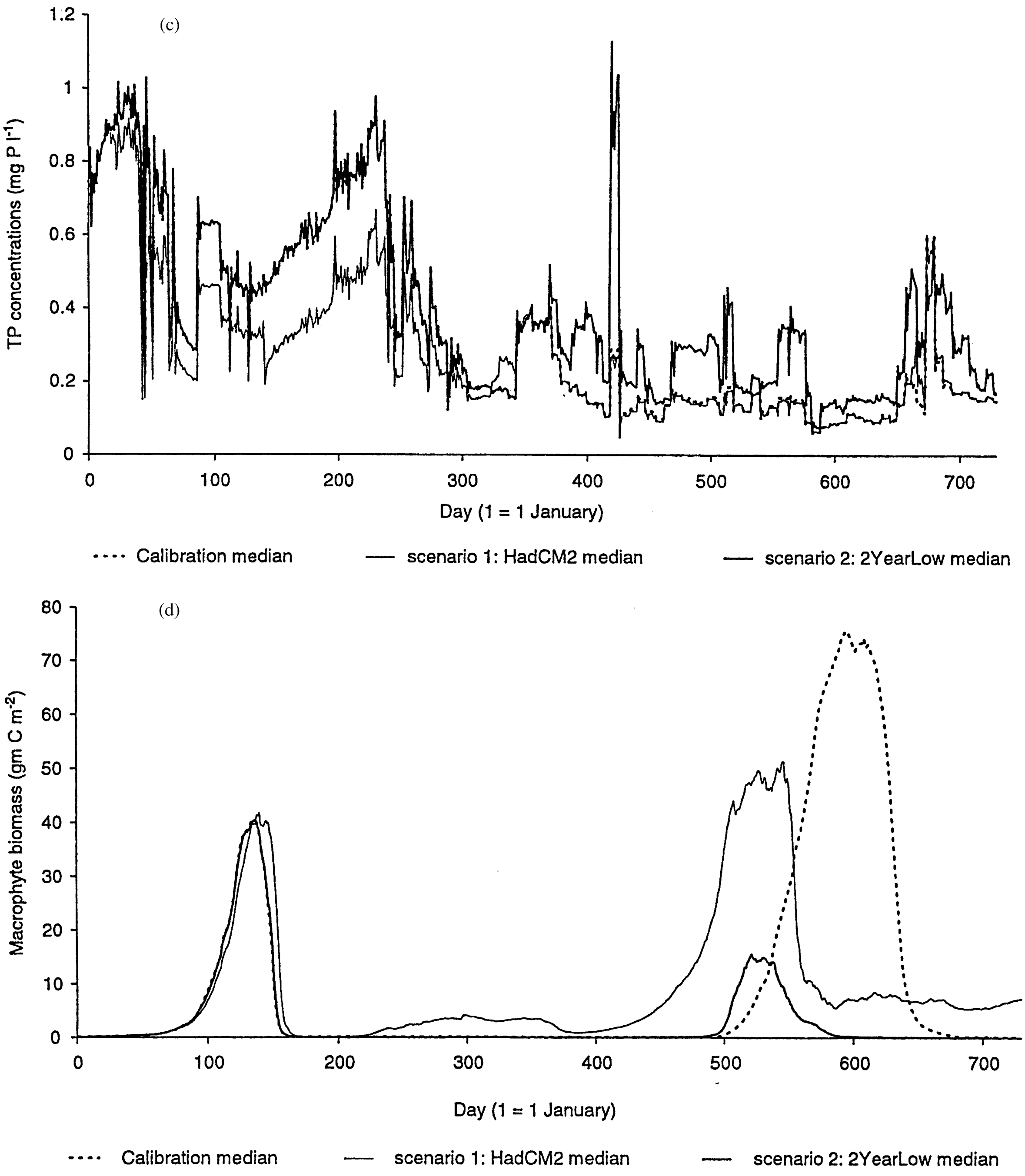

Fig. 3. (*Continued*).

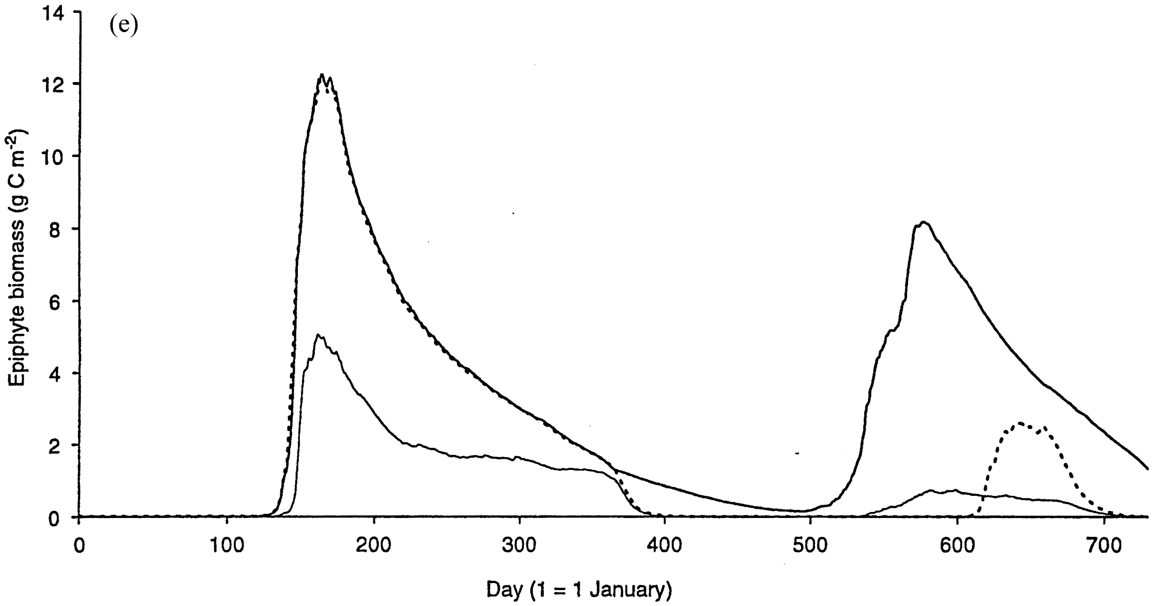

Fig. 3. (*Continued*).

occurs most probably because the biomass at the end of year 1 was higher than in the other two cases, and the equation describing the macrophyte growth is dependent on the macrophyte biomass (Table 3).

The timing of the peaks in the epiphyte biomass is dependant on the macrophyte growth, since the epiphytes can only establish themselves in the presence of macrophytes (Fig. 3e). The greatest peak in the epiphyte biomass occurs in year 1 during both model calibration and the scenario 2 simulations and, in both instances, the peaks correspond to the lowest flows and highest in-stream SRP and TP concentrations simulated. Following effluent treatment, in each of the 3 cases (calibration and scenario 1 and 2), the epiphyte biomass in year 2 is lower than the corresponding peak in year 1, in year 2 the simulated flows are higher in case of the model calibration and scenario 1, whilst the SRP and TP concentrations are lower in all three cases. In year 2, the greatest peak in the simulated epiphyte biomass occurs for scenario 2 when the modelled flows are lowest and the SRP and TP concentrations are highest of the three cases. The peak macrophyte biomass simulated in scenario 2 is only approximately 20% of the peak simulated during model calibration, which implies that the epiphytic growth is causal in the macrophyte decline.

The higher flows simulated in the spring and early summer in scenario 1 appear to limit epiphytic growth as the biomass reached is lower than in the other two cases, even though the SRP and TP concentrations are similar to the those simulated during model calibration. The simulated epiphytic growth, in scenario 1, occurs earlier than during calibration because the macrophyte biomass is higher in this case, and therefore, sufficient for the epiphytes to start growing whilst the epiphyte growth simulated during calibration occurs later in year 2 because the onset of macrophyte growth also occurs later in year 2.

If the low-flow time series is extended to 6 years, then the simulated results suggest that the epiphyte and macrophyte peak biomass decreases to approximately 6 and 10 g C m^{-2}, respectively (Fig. 4). Thus, the simulations suggest that even with lower in-stream TP and SRP concentrations

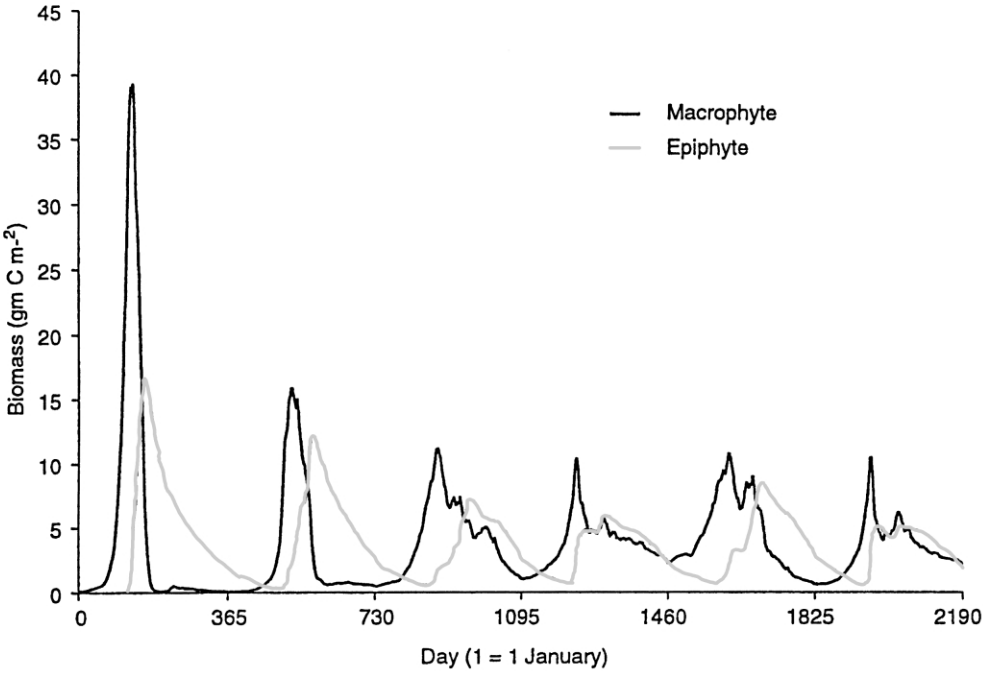

Fig. 4. Long term changes in the simulated (a) macrophyte and (b) epiphyte biomass in response to a 6-year succession of low flows.

due to effluent removal, then low flows could cause the macrophyte biomass to decline by approximately 75%.

5. Discussion

The work presented represents one of the first studies to simulate the impact of changing flow conditions on macrophyte growth in groundwater fed streams and rivers in the UK. Whilst there are many simplifications within the work, the study presents valuable insights into the possible outcomes of climate change on river ecology. Specifically, the results of the study begin to quantify the potential impacts of climate change on the macrophyte biomass of the River Kennet. However, the quantification of the changes in the macrophyte biomass must remain tentative given the structural and parameter uncertainty within the in-stream model. Nevertheless, the results provide a first approximation to the potential impacts of climate change and thereby provide a focus for discussion and a basis for future work.

From the results, it is evident that flow is more important than the current in-stream TP and SRP concentrations in controlling the macrophyte biomass, which is the same conclusion as that drawn from field studies (Ham et al., 1981). Flow controls the dilution of the SRP and TP input from the STW and, furthermore, flow also controls the macrophyte biomass directly through wash out and indirectly by controlling the epiphyte biomass. Based on the model results it is suggested that there may be two important flow thresholds with regard to macrophyte growth. The first threshold, lower than the second, relates to the removal of epiphytes from the system thereby allowing unrestricted macrophyte photosynthesis. The second threshold relates to the flow above, which macrophyte leaves and stems (and possibly whole plants) are washed from the reach.

The analysis of the results for the model calibration relating to 1997 and the extended low flow scenario (2) are important because the flows in 1997 were very low, only the flows observed in 1976 were lower in the recorded history of the River Kennet. As such, the simulations of the

1997 flows represent an extreme low-flow case that suggests epiphytic growth can increase rapidly and reach levels that have a detrimental effect on macrophyte growth, the lowest macrophyte peak biomass and the greatest epiphyte biomass occur in the second year following effluent treatment but when the flows are lowest (scenario 2). Thus, the major concern regarding the impacts of changed precipitation is not the shift in the seasonal patterns when the summers may become drier but winters become wetter, but the frequency of dry years. This is the most important result of the study given the output from current climate change models predict that drier years are likely to become more frequent, especially in the south-east of England (Hulme and Jenkins, 1998). As such, future work should be focused upon investigating the particular effects of a long sequence of dry years. Initial simulations suggest that the epiphyte biomass reaches a stable peak biomass for 6 years and therefore, the problem will persist whereby the macrophyte peak biomass will decline from that in year 1.

This is an important result in the context of managing groundwater abstraction management and defining eutrophication standards. Whilst obviously abstracting water during low-flow periods will lower flows, further placing stress on the river's plant and animal life, such abstraction may also encourage the epiphytic algal growth. If flow conditions did become lower then of major concern would be the increased growth of plants on the margins of the river, which may occur at the expense of *Ranunculus* at the river's edges. To some extent, this has been verified by the circumstantial evidence that arose during the Axford Public Enquiry, whereby local people had observed excessive epiphyte growth and reduced macrophyte growth during extended low-flow periods (Neal et al., 2002).

The results presented in this study regarding the growth of macrophytes and epiphytes must be considered as conjectures since they are based on model simulation, and therefore, are affected by the structural and parameter uncertainty within the model. In scenario 1, the simulated macrophyte growth occurs earlier in year 2 than during model calibration. As such, it may be expected that both the macrophyte and epiphyte biomass should be higher than those simulated during calibration. When the macrophyte biomass in scenario 2 peaks and then decreases the flows are lower and the solar radiation and water temperature higher than during the preceding period of growth. This possibly suggests a limitation in the equation that represents the relationship between the macrophytes and epiphytes using the Lotka–Volterra equation (Lotka, 1925; Volterra, 1926, Table 3). Consequently, the macrophyte death rate is dependent on the macrophyte biomass, and therefore, when this biomass is sufficiently high the macrophyte biomass can decline even if the solar radiation and water temperature are increasing. Whilst this is obviously a limitation to the model, the use of an equation based on the Lotka–Volterra idea of predicting the abundance of a species is a pragmatic solution to permit the development of the modelling approach taken, and allows a first approximation of the macrophyte growth in response to climate change scenarios to be derived. As knowledge of species competition improves then the representative equations can be encapsulated in the model.

To corroborate the simulation results further fieldwork needs to be done because work presented in the literature reporting the affects of flow on the macrophyte and epiphyte communities remains inconclusive. Some field and modelling studies suggest that flow does control macrophyte and epiphyte growth (Sand-Jensen, 1977; Phillips et al., 1978; Ham et al., 1981; Wade et al., 2002a) and a recent study suggests that *Ranunculus* grew back rapidly in a reach of the Kennet near the Savernake Forest downstream of the Marlborough STW in 1998 (Wright et al., 2002). However, another recent study highlights little relationship between epiphyte biomass and flow (Flynn et al., 2002). To improve the model, it is recommended that detailed monitoring of both macrophytes and epiphytes should be undertaken to assess the changes in their biomass in relation to flow and phosphorus concentrations. Ideally, such a study should be done just downstream of STW both before and after the removal of P from the final effluent. Such studies should also assess whether it is the flow or the localised turbulence around the macrophytes that is most important, possibly be relating biomass to Reynolds number. The effects of water temperature and solar radiation changes on plant growth need to be assessed. Recent reports suggest that macrophyte diversity may be very sensitive to temperature changes (Mainstone et al., 2000; Mainstone and Parr, 2002). Furthermore, future field and modelling studies should consider the biological influences on macrophyte growth, in addition to those resultant from chemical and physical factors. Such biological influences should include species competition and grazing of macrophytes by zooplankton.

Given the present uncertainty regarding flow-related controls on plant life and the strategic importance of assessing the effects of climatic variability on stream ecology there is a need for long-term biological and chemical data records to be collected. Such records must cover decades, or longer, given the climate variability is large and changing on a decadal or longer scale. For instance, in the 2 years covered by this study, both extreme low- and high-flow conditions were observed. At Marlborough, the lowest and highest monthly runoff totals since records began in 1972 were observed in January and November, respectively (NERC, 1998). Biological surveys are often missed from environmental studies where general water quality data is collected and this is a shortfall since general patterns of change cannot be assessed without cross-reference. The link between the current Kennet modelling studies and the active field research provides a clear indication of the value of a combined approach, as does a companion study of the River Thame (Cooper et al., 2002a,b; Gardner et al., 2002)

6. Conclusions

Assessing the impacts of phosphorus removal from sewage works under changing flow conditions on the water quality and biology remains an important issue, and clearly there is a need to continue to test and extend mathematical programmes such as the Kennet model to describe the changes occurring. Given the complexity of aquatic systems, then modelling approaches that incorporate the relevant processes through the balance of 'lumped' and 'distributed' approaches taken seem appropriate given they offer a balance between useful model output, reasonable process representation and pragmatic data requirements.

This simulation study has flagged that flow may be a major control on macrophyte and epiphyte growth in a single reach of the River Kennet. Thus, clearly it is important to consider the flow regime when assessing the potential impact of both point and diffuse source P inputs to a river system on the in-stream ecology. Clearly, many questions remain regarding the factors and processes that will be important in controlling the macrophyte and epiphyte biomass under changing flow conditions (Jarvie, 2002b). Despite this, the study has demonstrated the utility of a new water quality model that represents the current understanding regarding P and macrophyte dynamics in rivers. However, investigations of other aquatic systems are required. In particular, the Kennet Model needs to be scaled-up to simulate multiple reaches and diffuse source inputs in order to describe basin wide functioning. Furthermore, the present model should be applied to systems were the P concentrations are lower than those observed in the Kennet as such systems may be more sensitive to fluctuations in P concentrations.

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