

Periphyton dynamics in a floodprone prealpine river: evaluation of significant processes by modelling

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SUMMARY

1. Periphyton chlorophyll *a* was measured at weekly or 2 weekly intervals from October 1992 to March 1994 at four sites in a Swiss prealpine gravel bed river that was frequently disturbed by unpredictable spates.
2. To evaluate the dominant processes that control periphyton biomass, measured data were compared with a set of simulations from an empirical dynamic periphyton model. Different combinations of process hypotheses were systematically activated and deactivated in order to assess their importance.
3. The simplest model leading to an acceptable agreement with measured data employs a biomass-dependent growth rate, a detachment rate directly proportional to discharge and biomass, and a catastrophic loss rate during bed moving spates. Terms describing light or temperature dependence had a minor effect on the model fit.
4. The model describes the temporal pattern of the periphyton biomass as a series of growth curves periodically truncated by spates. Within the uncertainties of the measurements, mainly caused by the spatial heterogeneity of periphyton, the biomass recovered along deterministic trajectories.
5. Sensitivity analyses with respect to model parameters and model structure showed that site-specific model parameters could not be unequivocally determined, and that the model yields similar results with slightly different formulations of processes. This indicates that the data base with respect to periphyton biomass was too small for a unique identification of model details but that the main conclusions on the significance of processes did not depend on arbitrary choices of the model formulation.

Introduction

A major factor limiting the accumulation of periphyton (epilithon) in gravel bed rivers are flows that cause loss of biomass by increasing shear stress, physical abrasion by suspended solids, and abrasion by moving substrata (Tett *et al.*, 1978; Fisher *et al.*, 1982; Biggs & Close, 1989; Uehlinger, 1991; Biggs & Thomson, 1995). After such disturbances biomass accrual is a function of the growth of the surviving and colonizing algae, and of the current induced drag. The rate of colonization depends on the number and proximity of refugia, and on the immigration properties of colonizers (Kaufman, 1979; Stevenson, 1990; Peterson & Stevenson, 1991). The growth rate is controlled by light, temperature and the availability of nutrients

(Triska *et al.*, 1983; Bothwell, 1986, 1988, 1989). 'Biotic' losses such as grazing and autogenic sloughing may become major constraints of biomass accrual only after long periods without spates, because recovery of the invertebrates is usually slow compared with periphyton growth, and loss by autogenic sloughing is expected to become important only as the community ages (Fisher *et al.*, 1982; Biggs & Close, 1989; Power, 1992). Multiple linear regression analysis has shown that a few parameters such as time since spate, mean discharge and maximum discharge during the spate can explain > 60% of the variance in periphyton biomass of streams (Biggs, 1988; Fisher & Grimm, 1988; Biggs & Close, 1989; Uehlinger, 1991). This has

highlighted the importance of physical control of periphyton biomass dynamics in streams. The long-term dynamics of biomass have been conceptualized in models by Reichle, O'Neill & Harris (1975), Fisher & Grimm (1991) and Power (1992).

McIntire (1973), McIntire & Colby (1978) and Horner *et al.* (1983) have developed simulation models for periphyton dynamics in laboratory streams which include parameters to account for the individual growth and loss processes. The McIntire (1973) and McIntire & Colby (1978) models utilize light, temperature and nutrients to control growth. Loss of biomass occurs by current-induced scouring, water velocity and temperature-dependent respiration and grazing. Horner *et al.* (1983) described the periphyton accrual rate as a function of the difference between maximum sustainable biomass and actual biomass, the phosphorus uptake rate, and water velocity and light. This model, originally calibrated in artificial channels, has been used to predict the effects of changes in stream nutrient loading by Welch *et al.* (Welch, Horner & Patmont, 1989; Welch, Quinn & Hickey, 1992). However, differences between model predictions and periphyton data were remarkably high, presumably due to uncertainties with respect to the assessment of spatial and temporal variation in nutrient concentrations, velocity, temperature, grazing pressure, light climate and properties of the substrata. Rodriguez (1987) and Momo (1995) presented logistic growth models that also included colonization. The determination of the maximum sustainable biomass, a key parameter of logistic models, can be very difficult if frequent disturbances truncate growth curves before saturation becomes evident. None of the models considers catastrophic loss of biomass during spates, a fundamental process in streams and rivers.

The present study was undertaken to identify processes which control the periphyton dynamics in a floodprone river. For this the model of McIntire (1973) was modified and used as a 'hyper'-model considering the dependencies of periphyton growth and detachment on internal and external variables that were thought to be important for periphyton dynamics in natural rivers. These variables were incident light, water temperature, biomass and discharge. Nutrients were not included because definitive measures of nutrient limitation were lacking for the investigated river, and previous data on phosphorus and nitrogen concentrations suggested that these nutrients were not

Table 1 Descriptors of the disturbance regime of the River Necker. The database are discharge records of the Swiss Hydrological and Geological Survey at km 8.2 from 1974 to 1993

	Maximum discharge during spate*		
	> 14 m ³ s ⁻¹	> 28 m ³ s ⁻¹	> 40 m ³ s ⁻¹
Recurrence interval (days)			
minimum	1.2	2.4	2.9
median	11.5	21.9	38.2
maximum	121.3	204.8	234.1
Spate frequency (no. of spates per year)	18.9	10.5	6.3
Predictability indices† according to Collwell (1974)			
Predictability <i>P</i>	0.293	0.134	0.126
Constancy	0.292	0.057	0.046
Contingency	0.001	0.081	0.080

*Discharge data were multiplied by 1.4 to account for the larger catchment area of the study site compared with the catchment upstream of the gauging station (Spreafico *et al.*, 1992).

†The annual cycle was divided in monthly intervals, and two levels of intensity, *spate* and *no spate*, were distinguished.

limiting, at least at the surface of mats (Uehlinger, 1991). The significance of the variables was tested by systematically 'turning on and off' the model processes controlled by these variables.

Study site

The prealpine region of Switzerland covers an area between the Swiss Plateau and the Alps. Altitudes range up to 1800 m a.s.l. The River Necker, a sixth-order river in the eastern part this prealpine region, drains a catchment of 126 km² of which about one-third is forested. The mean annual discharge at the study site is 4.6 m³ s⁻¹. The flow regime is rather unpredictable (Table 1). Bed moving spates may occur at any time of the year, but usually last for less than half a day. At the study reach (km 0.87–3.00; 553–565 m a.s.l.) gravels and cobbles cover more than 90% of the channel area. The channel slope within the reach averages 0.6%. Steep valley slopes limit the extension of the floodplain to a maximum of 50 m. There was no direct shading of the sampling areas by riparian vegetation. At base flow riffles and runs formed about 85% of the wetted channel. Inflow of treated sewage upstream of the study site, and agricultural runoff, raise concentrations of soluble reactive phosphorus (SRP) and inorganic nitrogen

Table 2 Nutrient concentrations in the Necker at km 0.8 measured between 1992 and 1994, $n = 38$ (Frutiger EAWAG, unpublished)

	SRP ($\mu\text{g l}^{-1}$)	$\text{NO}_3\text{-N}$ ($\mu\text{g l}^{-1}$)	$\text{NO}_2\text{-N}$ ($\mu\text{g l}^{-1}$)	$\text{NH}_4\text{-N}$ ($\mu\text{g l}^{-1}$)	Si ($\mu\text{g l}^{-1}$)
First quartile	17	1047	3	7	2463
Median	23	1273	5	13	3205
Third quartile	30	1483	6	249	3715

compounds to rather high values (Table 2). The transition from nutrient saturation to nutrient limitation has been reported to be in the range of 0.6–15 $\mu\text{g SRP l}^{-1}$ for inorganic phosphorus and from 50 to 60 $\mu\text{g l}^{-1}$ for inorganic nitrogen compounds (e.g. Grimm & Fisher, 1986; Bothwell, 1989; Newbold, 1992). These limits are usually lower than the corresponding concentrations at the study site. However, more reliable indicators of nutrient limitation are missing, such as phosphorus or nitrogen cell quota or alkaline phosphatase activity (Healy, 1975) for the River Necker.

Methods

Discharge data were obtained from a gauging station of the Swiss National Hydrological and Geological Survey, 5.2 km upstream of the study reach. The measured values were multiplied by a factor of 1.4 to correct approximately for the larger catchment area of the study site (Spreato *et al.*, 1992). A spate was defined as increase in flow exceeding ten times the mean daily flow, which is exceeded on 329 days of a year (Q_{329}). Estimates of Q_{329} ($0.78 \text{ m}^3 \text{ s}^{-1}$) are based on discharge records from 1972 to 1993. If the time between two consecutive flow peaks was less than 1 day, or the minimum flow between two consecutive peaks exceeded Q_{329} , the spates were combined to one event. Water temperature was recorded at 30-min intervals with a datalogger (Tattletale VI, single-card datalogger, Onset Computer Corp.). Incident light was recorded at km 3 (about 200 m from the channel) as photosynthetically active radiation (PAR) using a LI-190SA quantum sensor and a LI-1000 datalogger (LI-COR Inc. Lincoln, Nebraska).

From October 1992 to the beginning of January 1993 periphyton was monitored at two riffles/runs and two pools. Because the pool sites could not be sampled when flow exceeded $4\text{--}5 \text{ m}^3 \text{ s}^{-1}$ they were replaced by two further riffle/run sites for the rest of the sampling

period until March 1994. The pool data were used for the subsequent evaluation of the model. Samples were taken every 2 weeks. Fourteen to twenty stones were collected without 'conscious bias' (Leopold, 1970). On several dates two riffles were sampled at shorter intervals to get information on the immediate impact of spates on the periphyton. To obtain periphyton samples the stones were scrubbed with a wire brush into a bucket with water, then the a, b and c dimensions of the stones were measured (Uehlinger, 1991). Aliquots of the suspensions were filtered on glass fibre filters (Whatman GF/F) for the subsequent determination of chlorophyll *a*. Chlorophyll *a* was determined by HPLC after extraction with hot ethanol (Meyns, Illi & Ribic, 1994). Area values of chlorophyll *a* were calculated for each site as described by Uehlinger (1991).

To identify relevant process or external parameters for periphyton dynamics measured periphyton biomass was compared with simulations of a 'hyper'-periphyton model in which combinations of processes were systematically activated or inactivated. To evaluate whether a process or parameter is significant all results of such trials must be considered (Caswell, 1976). This is important because 'the good fit of the best fitting model should not be surprising' (Chatfield, 1995).

Model simulations, parameter estimation and sensitivity analyses were performed with the computer program AQUASIM (version 1.0a), which is designed for the identification and simulation of aquatic systems (Reichert, 1994a,b, 1995). Parameter estimations of a given model are based on the minimization of χ^2 (eqn 1):

$$\chi^2 = \sum_{i=1}^n \left(\frac{X(t_i) - X_{meas,i}}{\sigma_{meas,i}} \right)^2 \quad (1)$$

where $X_{meas,i}$ is the biomass measured at the time t_i , $X(t_i)$ is the biomass at the time t_i calculated with the model, $\sigma_{meas,i}$ is the standard deviation of $X_{meas,i}$, and n is the number of observations.

The evaluation of model fits is based on the final value of χ^2 and on the number of sign changes of the residuals. χ^2 characterizes the size of the deviation between the model and the data, and the number of sign changes systematic deviations (significantly less sign changes than $n/2$ indicate systematic deviations of $X(t_i)$ from $X_{meas,i}$) (Söderström & Stoica, 1989).

The sensitivity analysis of parameters is based on the sensitivity function $\delta_{X,p}$ (eqn 2)

$$\delta_{X,p} = p \frac{\partial X}{\partial p} \quad (2)$$

which calculates the linear approximation to the change of the periphyton biomass, X , resulting from a 100% change of a selected parameter, p . Large values of $\delta_{X,p}$ indicate a strong dependence of X on p that allows an accurate identification of p , if there is no strong correlation of p with other parameters. If two sensitivity functions have a similar shape, changes in X caused by changes in one parameter can be approximately compensated for by appropriate changes in the other. In this case (or in an analogous situation with an approximate linear dependence of more than two sensitivity functions) the determination of parameters may be uncertain (this is also the case when the values of the sensitivity functions are large with respect to these parameters). Because there exists no single 'true' periphyton model, but several adequate simplifying descriptions of the complex real system, the significance of process formulation should also be evaluated. Therefore, a structural sensitivity analysis was done. For this, different formulations were used for the most important processes and the results (χ^2) of the corresponding simulations compared.

Model description

The periphyton model is given by eqns 3 and 4:

$$\begin{aligned} \frac{dX}{dt} = & \underbrace{\mu_{max,0} X}_{1a} \underbrace{\frac{1}{1 + K_{X,inv} X}}_{1b} \underbrace{\frac{I}{K_I + I}}_{1c} \underbrace{\exp(\beta(T - T_0))}_{1d} \\ & - \underbrace{c_{det} Q(X - X_0)}_{2a} - \underbrace{k_{flood}(Q)(X - X_0)}_{2b} \end{aligned} \quad (3)$$

with

$$k_{flood}(Q) = \begin{cases} 0 & \text{for } Q < Q_{crit} \\ k_{cat} & \text{for } Q \geq Q_{crit} \end{cases} \quad (4)$$

In these equations X is the periphyton biomass (mg Chl a m^{-2}) and t is time (days). The terms labelled with '1' describe net growth, which also includes decay, loss by grazing and discharge-independent

detachment. The flow-induced loss processes are labelled with '2':

1 Term 1a: This first term describes periphyton growth rate as a linear process in biomass which results in an exponential increase in biomass. The coefficient $\mu_{max,0}$ is the maximum specific growth rate (d^{-1}) at the reference temperature T_0 . This maximum net growth rate is altered by the terms 1b–1d that account for the effects of density limitation (1b), light (1c) and temperature (1d) as described below.

2 Term 1b: this characterizes the biomass limitation of the growth rate. At low values of X the product of term 1a and term 1b is approximately $\mu_{max,0} X$ which results in exponential increase in biomass. If X is much larger than $1/K_{X,inv}$ then the product of term 1a and 1b becomes independent of X , which results in a linear increase in biomass with time. Flume experiments show that mat growth rates slow down with increasing biomass (McIntire & Phinney, 1965; Bothwell, 1989). One explanation for this phenomenon is that in a periphyton mat of increasing thickness only the primary production of the cell layers at the surface is supported by favourable light and nutrient conditions, whereas the productivity of inner layers is subject to increasing light and nutrient limitation (McIntire, 1973; Jasper & Bothwell, 1986). We disregarded the use of a logistic growth equation in order to separate growth from flow induced detachment processes and to avoid the problem of determining the maximum sustainable biomass, as this parameter cannot be obtained from (spatially) truncated growth curves. The terms 1a and 1b depict an unusual parameterization of a Monod-type rate expression which allows us to switch to the default model (exponential growth in X) by setting the inverse half saturation constant $K_{X,inv} = 0$. At $X = 1/K_{X,inv}$ the growth rate is half of its maximum value of:

$$r_{max,0} = \frac{\mu_{max,0}}{K_{X,inv}} \quad (5)$$

The dimension of $K_{X,inv}$ is mg Chl a m^{-1} . The formulation of biomass limited growth given by terms 1a and 1b is the same as that suggested by McIntire (1973).

3 Term 1c: this accounts for the influence of seasonal variations in light on the growth rate. A Monod-type formulation is used where I is the daily integrated light intensity (E m^{-2}) and K_I (E m^{-2}) the half-saturation coefficient. A different formulation of the light saturation as, for example, a hyperbolic tangent function (Jassby & Platt, 1976) would lead to a similar result.

The light dependence is inactivated by setting $K_I = 0$. Light inhibition effects are not considered.

4 Term 1d: this approximation to the Arrhenius or van t'Hoff equation accounts for the influence of the seasonal temperature changes on the growth rate. T is the mean daily temperature ($^{\circ}\text{C}$), T_0 is the reference temperature set equal to 20°C , and β is the coefficient of temperature dependence of growth ($^{\circ}\text{C}^{-1}$). By setting $\beta = 0$ temperature dependence is inactivated.

5 Term 2a: this describes the detachment rate as a smoothly increasing function of discharge and biomass of the periphyton mat (McIntire, 1973; Biggs & Close, 1989; Uehlinger, 1991; Peterson & Stevenson, 1992). The detachment rate here is assumed to be proportional to the product of discharge Q ($\text{m}^3 \text{s}^{-1}$) and biomass X exceeding the minimal biomass X_0 (the parameter X_0 is discussed in the following paragraph). c_{det} is an empirical detachment coefficient ($\text{s m}^{-3} \text{d}^{-1}$). The process can be inactivated by setting $c_{det} = 0$. The term 2a can be used straightforwardly, because discharge data are usually available. More mechanistic formulations of the detachment function may use bottom shear stress, but they would depend on assumptions of the friction formula and channel geometry.

6 Term 2b: this describes the catastrophic loss of biomass during bed moving spates. Owing to the high value of k_{cat} ($= 100 \text{ d}^{-1}$, eqn 4) the periphyton biomass rapidly approaches the minimal value X_0 for all but the extremely short spates. The minimal biomass X_0 allows the periphyton community to recover after the event. In the present model the value of X_0 is independent of the magnitude of the spate. An alternative to X_0 with approximately the same effect would be the use of a small colonization rate. The critical discharge for the onset of bed load transport, Q_{crit} , is $40 \text{ m}^3 \text{ s}^{-1}$ (see results). The process can be inactivated by setting Q_{crit} to the unrealistically high discharge of $1000 \text{ m}^3 \text{ s}^{-1}$.

To perform simulations the initial periphyton biomass, X_{ini} , where $X_{ini} \geq X_0$ must be specified in addition to the model parameters described above. As noted previously, the effects of temporal changes in nutrient limitation on the periphyton growth are not explicitly included in the present model. Nutrient dependence of growth could be added as a term 1e to eqn 3 (cf. McIntire, 1973). Similarly, grazing can

be included explicitly as an additional loss term 2c, if information on grazing is available.

Results

Temperature, light and discharge

Mean daily water temperatures ranged from 0 to 20°C (Fig. 1a). Incident daily integrated light intensity showed higher day to day variations than temperature (Fig. 1b). Seasonal temperature patterns were less regular than corresponding PAR patterns but, apart from a small phase shift, PAR and temperature show a quite similar seasonal pattern. During spates with maximum discharge $Q_{max} > 40 \text{ m}^3 \text{ s}^{-1}$, the uppermost sediments were moved or subject to abrasion by moving sediments. Such events, not equally spaced in time, occurred fourteen times during the 18-month investigation period (Fig. 1c). Less severe spates ($28 \text{ m}^3 \text{ s}^{-1} < Q < 40 \text{ m}^3 \text{ s}^{-1}$) caused local scouring or aggradation of pools or riffle/runs.

Periphyton biomass

Biomass was measured on forty-three occasions. The temporal pattern of chlorophyll *a* reflected the timing and frequency of bed moving spates (Fig. 1d). Spates with $Q_{max} > 40 \text{ m}^3 \text{ s}^{-1}$ eliminated periphyton almost completely. During periods of low flow (February/March and November/December 1993) periphyton biomass reached more than $200 \text{ mg Chl } a \text{ m}^{-2}$. These dense communities suffered distinct losses (55–60%) by relatively small spates ($Q_{max} \approx 14 \text{ m}^3 \text{ s}^{-1}$) as on 17 March and 13 December 1993.

Correlations between biomass and discharge related parameters were highly significant (Table 3). Stepwise multiple regression analysis showed that average discharge and time since the last spate of $Q_{max} > 14 \text{ m}^3 \text{ s}^{-1}$ explained 56% of the variation in chlorophyll *a*. No significant correlation existed between chlorophyll *a* and temperature or PAR. These descriptive statistics indicate that the temporal variation of periphyton biomass is strongly influenced by the hydrological parameters.

Evaluation of the periphyton model

The model was evaluated (eqns 3 and 4) by systematically activating or deactivating growth and loss

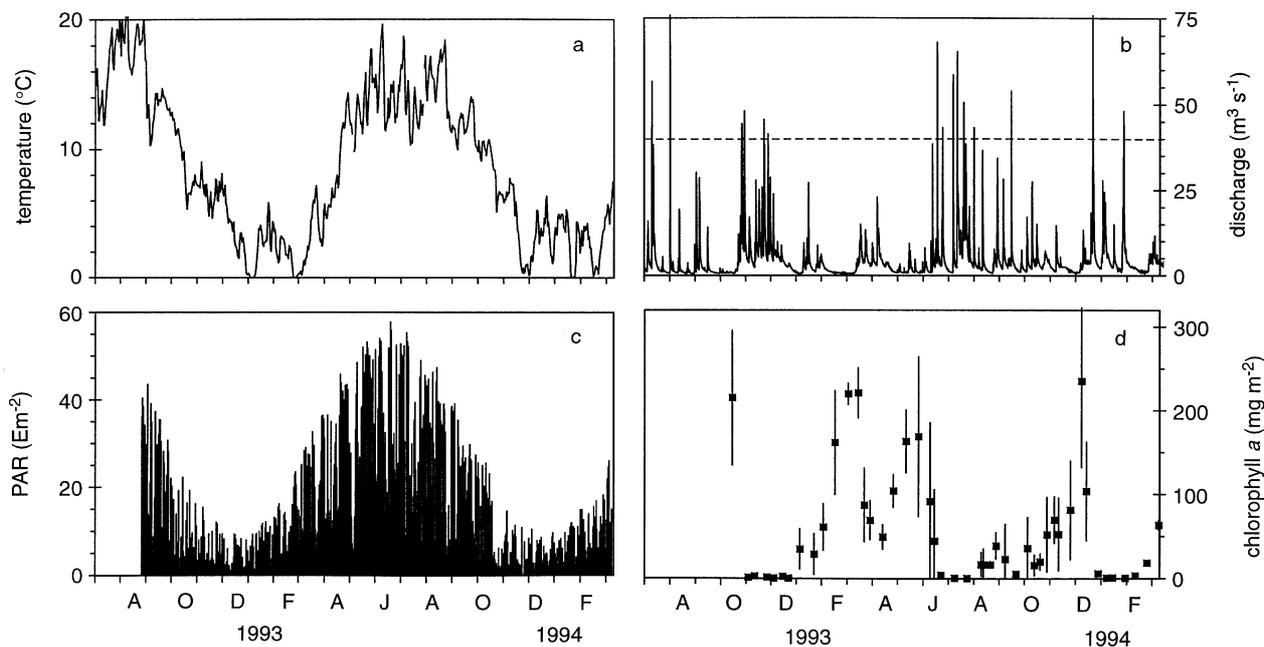


Fig. 1 Seasonal changes in water temperature (a), light (b), discharge (c) and periphyton biomass (d) at the study reach. The dashed line on panel (c) indicates the critical discharge for bed load transport throughout the study reach. Vertical bars in (d) = standard deviation.

Table 3 Correlation analysis of periphyton chlorophyll *a* (mg m⁻²) (*n* = 43) with average inter-sampling discharge (Q_{avg}) and temperature (T_{avg}), days since last spate where maximum flow (Q_{max}) exceeded 14, 28 and 40 m³ s⁻¹, and cumulative PAR during preceding sampling interval (PAR_{cum})

	Q_{avg}	Days since last spate			T_{avg}	PAR_{cum}
		$Q_{max} > 14 \text{ m}^3 \text{ s}^{-1}$	$Q_{max} > 28 \text{ m}^3 \text{ s}^{-1}$	$Q_{max} > 40 \text{ m}^3 \text{ s}^{-1}$		
R^2	-0.38	0.52	0.46	0.41	-0.002	0.029
P	<0.001	<0.001	<0.001	<0.001	NS	NS

functions. This led to a series of calculations of different model complexity. The results of this procedure are summarized in Table 4. Combinations which included both light and temperature terms were not considered because the strong correlation between light and temperature data did not allow separation of the effects of both parameters (cf. Fig. 1a and b).

Models with two or three parameters (fits 1–6) failed to describe the periphyton dynamics (Fig. 2a and b show the results of fits 1 and 6). The models with four parameters (fits 7–15) fits 9, 10 and 15 that considered two of the three processes of biomass limited growth rate, continuously increasing detachment with discharge and catastrophic loss resulted in a more significant decrease of χ^2 compared with the other fits (Table 3, fits 9, 10 and 15 shown

in Fig. 2c–e). At the level of the five parameter models (fits 16–22) the model combining the three processes biomass limited growth, continuously increasing detachment with discharge and catastrophic loss during spates (fit 20, Fig. 2f) provided the best simulation of the periphyton dynamics. The additional activation of the light or temperature dependence (fits 23 and 24) did not significantly improve fit 20. With exception of fits 20, 23 and 24 the values of χ^2 indicate significant deviations between calculation and measurements (significance level $P < 0.001$). The smallest values of χ^2 (20, 23 and 24) coincided with the largest number of sign changes of the residuals (Table 5). The fact that the processes 1b, 2a and 2b had the largest influence on χ^2 through all levels of model complexity substantiate the reliability of fit 20 (Table 5).

Table 4 Results of parameter fits (minimization of χ^2) of the model defined by eqns 3 and 4. The fits are ordered with increasing number of active processes. Column 1 contains the number of the fit, column 2 the number of fitted parameters, columns 3–9 the final parameter values. Empty cells mark the parameters set to zero and not included in a fit (zero values in the table means that the result of a fit is zero). Column 10 contains the value of the critical discharge for catastrophic loss of biomass. A value of $1000 \text{ m}^3 \text{ s}^{-1}$ inactivates this process, because discharge does not reach such a high value. The last two columns contain the value of χ^2 and the number of sign changes of the residuals

Fit	No. pars	X_{ini} mg Chl <i>a</i> m^{-2}	$\mu_{max,0}$ d^{-1}	$K_{X,inv}$ mg Chl $\text{a}^{-1} \text{m}^2$	K_I E d^{-1}	β $^{\circ}\text{C}^{-1}$	c_{det} $\text{s m}^{-3} \text{d}^{-1}$	X_0 mg Chl <i>a</i> m^{-2}	Q_{crit} $\text{m}^3 \text{s}^{-1}$	χ^2	Sign changes
1	2	0.490	0.00276						1000	1213.9	4
2	3	0.498	0.0027	0					1000	1213.9	4
3	3	0.498	0.0027		0				1000	1213.9	4
4	3	0.498	0.0027			0			1000	1213.9	4
5	3	0.987	0.0402				0.00801		1000	1204.7	4
6	3	212	0.0257					0.168	40	979.8	10
7	4	0.498	0.0027	0		0			1000	1213.9	4
8	4	0.649	0.00193	0.00243		-0.00561			1000	1213.9	4
9	4	210	0.502	0.0116			0.0876		1000	279.2	4
10	4	205	0.363	0.257				0.00286	40	529.5	8
11	4	0.987	0.0402		0		0.00801		1000	1204.7	4
12	4	211	0.0257		0			1.68	40	979.8	10
13	4	68.2	0.023			-0.110	0.0276		1000	893.6	6
14	4	228	0.0009			-0.205		1.57	40	848.0	9
15	4	198	0.124				0.0413	1.57	40	460.3	10
16	5	202	1.11	0.0168	1.73		0.149		1000	250.8	14
17	5	209	0.845	0.508	1.73			0.00001	40	477.6	12
18	5	6.33	0.00783	0.0162		-0.178	0.0167		1000	272.1	10
19	5	216	0.674	0.444		0.0050		0.00001	40	495.7	11
20	5	212	0.573	0.0700			0.0224	0.000044	40	64.8*	16
21	5	198	0.124		0		0.0411	1.51	40	460.3	10
22	5	201	0.0684			-0.0537	0.0294	1.51	40	423.6	10
23	6	247	0.377	0.0364	1.21		0.0217	0.0188	40	63.1*	17
24	6	212	0.573	0.0700	0	0.0224	0.000044		40	64.8*	16

* $\chi^2 < \chi^2_{0.001}$

Sensitivity analysis

The sensitivity functions of the periphyton biomass (eqn 2) with respect to all parameters of the model used for fit 20 (Table 4) are given in Fig. 3. The periphyton biomass X was not sensitive to X_{ini} because soon after the beginning of the simulation (22 October 1992) the first bed moving spate reset the biomass to X_0 , that is assumed to be independent of the pre-spate biomass. During the early (exponential) growth phase the biomass is linearly dependent on X_0 but exponentially on $\mu_{max,0}$. Therefore, X responds less sensitively to changes in X_0 than in $\mu_{max,0}$ (Fig. 3). X is very sensitive to changes in $\mu_{max,0}$, $K_{X,inv}$ and c_{det} . However, $\mu_{max,0}$ and $K_{X,inv}$ are strongly correlated (Fig. 3; Table 6). This correlation indicates a strong dependence of X on the maximum growth rate $r_{max,0}$ (eqn 5, increasing $\mu_{max,0}$ and $K_{X,inv}$ by the same factor does not change the maximum growth rate, $r_{max,0}$). The correlation of

X_0 with $\mu_{max,0}$ and $K_{X,inv}$ (Table 6) is not apparent in Fig. 3, because the values of the sensitivity function with respect to X_0 are very small (Fig. 3). This analysis showed why the model parameters could not be accurately determined with the available data.

For the structural sensitivity analysis of the model terms 1b and 2a were varied as described in Table 7. Term 1b': the exponential relationship is an alternative formulation in describing the change from exponential growth to density limited growth to the generally used hyperbolic function (1b).

Rationales for the following alternative formulations for term 2a were:

1 Term 2a': detachment is assumed to be a process which is proportional to the bottom shear stress. Based on the Manning–Strickler friction law for a rectangular channel the bottom shear stress should vary with $Q^{3/5}$ (Chow, 1959; Henderson, 1966). A rectangular channel is a reasonable approximation for the study

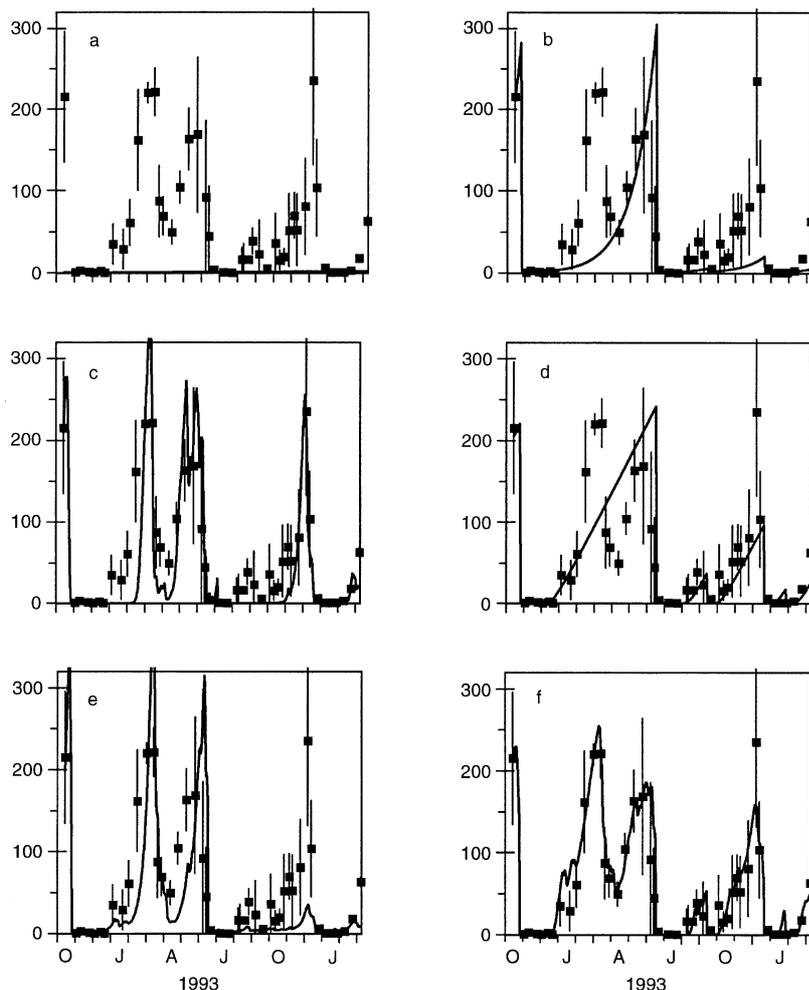


Fig. 2 Comparison of measured chlorophyll *a* ($\text{mg Chl } a \text{ m}^{-2}$, vertical bars = standard deviations) and calculated values (solid lines) for some fits with the model given by eqn 1 (the fits are defined in Table 4): (a) fit 1, (b) fit 6, (c) fit 9, (d) fit 10, (e) fit 15 and (f) fit 20.

reach; an increase of Q from 0.7 to $5.6 \text{ m}^3 \text{ s}^{-1}$ augments the average width of the wetted channel by only 30%.
2 Term $2 a'$: this accounts for the fact that concentration and abrasive impact of suspended particles increase with discharge. To account for the loss of periphyton by abrasion and bottom shear stress a detachment proportional to Q^2 was tried.

3 Term $2 a''$: detachment may increase more rapidly with growing thickness of the periphyton mat than described by term $2a$. To account for such an enhanced loss it was assumed that detachment was proportional to the square of X .

The outcome of the analysis (Table 7) confirms that fit 20 is the most parsimonious fit that led to a good agreement between calculated and measured biomass data, and it shows that neither biomass limitation of growth, nor biomass detachment as a function of discharge, were sensitive to slight modifications of the process formulation. The results indicate that details

of model formulation cannot be tested with a relatively small data base (forty-three measurements of the periphyton biomass), but they corroborate that the dominant processes have been identified.

Discussion

To evaluate the dominant processes which determine the temporal variation of the periphyton biomass in the floodprone River Necker, measured data was compared with models of increasing complexity by systematically including different combinations of proposed dependencies. The result of this procedure is in accordance with the assumption that growth and flow mediated loss control the biomass in this 'disturbance controlled' system (Uehlinger, 1991). By considering density-limited growth, a smooth increase in the detachment rate with discharge and a catastrophic loss during bed moving spates, the dominant temporal

Table 5 Decrease in χ^2 (columns 2–6) resulting from the subsequent consideration of additional processes (eq 1). The first column contains the fit number. The number of the model that considers this additional process is given in parentheses for each case. Changes in χ^2 which exceed 150 are bold. The distribution of these large changes emphasize the dominance of the processes 1b, 2a and 2b over the processes 1c and 1d

Fit	Decrease in χ^2 due to consideration the following terms of equation 1				
	1b Density limited growth	1c Light dependence	1d Temperature dependence	2a Flow-induced detachment	2b Catastrophic loss during spates
1	0.0 (2)	0.0 (3)	0.0 (4)	9.2 (5)	234.1 (6)
2	—	0.0 (7)	0.0 (8)	934.7 (9)	684.4 (10)
3	0.0 (7)	—	—	9.2 (11)	234.1 (12)
4	0.0 (8)	—	—	320.3 (13)	365.9 (14)
5	925.5 (9)	0.0 (11)	311.1 (13)	—	744.4 (15)
6	450.3 (10)	0.0 (12)	131.8 (14)	519.5 (15)	—
7	—	—	—	963.1 (16)	736.3 (17)
8	—	—	—	941.8 (18)	718.2 (19)
9	—	28.4 (16)	7.1 (18)	—	214.4 (20)
10	—	51.9 (17)	33.8 (19)	464.7 (20)	—
11	953.9 (16)	—	—	—	744.4 (21)
12	502.2 (17)	—	—	519.5 (21)	—
13	621.5 (18)	—	—	—	470.0 (22)
14	352.3 (19)	—	—	424.4 (22)	—
15	395.5 (20)	0.0 (21)	36.7 (22)	—	—
16	—	—	—	—	187.7 (23)
17	—	—	—	414.5 (23)	—
18	—	—	—	—	207.3 (24)
19	—	—	—	430.9 (24)	—
20	—	1.7 (23)	0.0 (24)	—	—
21	397.2 (23)	—	—	—	—
22	358.8 (24)	—	—	—	—
23	—	—	—	—	—
24	—	—	—	—	—

pattern of the periphyton biomass can be described as a series of growth curves periodically truncated by spates. Light or temperature dependence of the periphyton growth rate was apparently much less important than the above-mentioned processes.

The overall temporal pattern of the periphyton biomass reflected the impact of bed moving spates which reduce the biomass to rather low densities. Such events are often temporally clustered, consequently periods of low biomass may last for weeks as in October/November 1992 and June/July 1993. Owing to the strong correlation of the parameters a unique estimation of model parameters is difficult. This is not surprising because in the most successful model (fit 20, Table 4), five parameters had to be identified with only forty-three measured data points. However, it should be noted that none of the models with less parameters and none of the other five parameter models led to a similarly good fit (Table 4).

The role of smaller spates depends on their intensity (measured as discharge) and pre-flood biomass (Biggs & Close, 1989; Uehlinger, 1991). Their impact on the biomass is particularly evident when biomass densities are high (March and December 1993). In the present model, increasing discharge (i.e. increasing average current velocity) always results in a reduction of the net mat growth rate $k = X^{-1} dX/dt$ (eqn 3). However, the extent of this reduction is a function of discharge and density of the periphyton biomass; the flow required for detachment ($k < 0$) decreases with increasing biomass (Fig. 4). In gravel bed rivers the extent of the loss in biomass by spates has been shown to be a function of the biomass density and magnitude of the spate (Biggs & Close, 1989; Uehlinger, 1991). Horner *et al.* (1990) also demonstrated that chlorophyll accrual was positively correlated with velocity up to a threshold above which sloughing kept chlorophyll densities distinctly lower. It can be assumed that the wide range

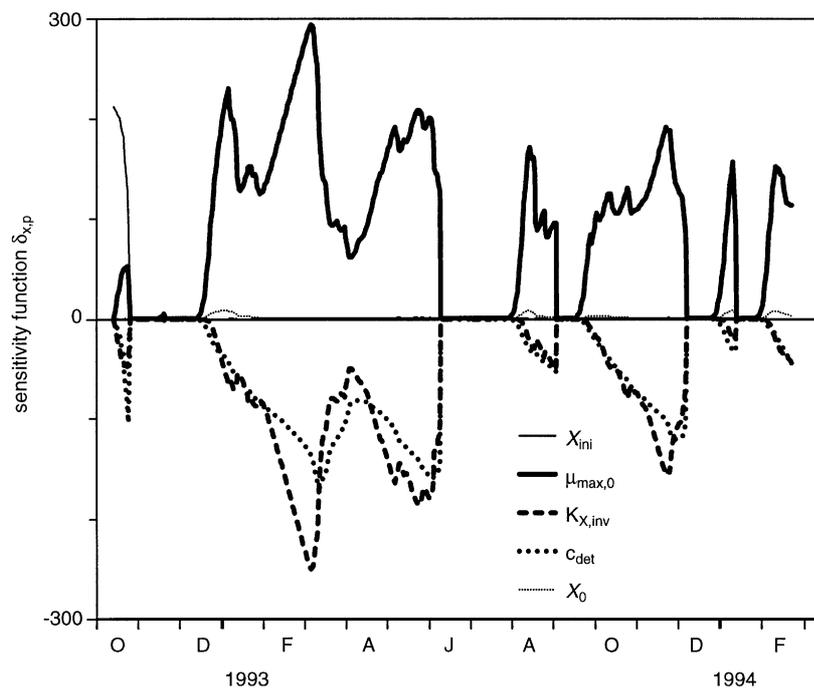


Fig. 3 Sensitivity functions (according to eqn 5) of periphyton biomass for fit 20 with respect to the parameters X_{ini} , $\mu_{max,0}$, $K_{X,inv}$, c_{det} and X_0 .

Table 6 Correlation matrix and estimated standard deviations for fit 20 of the model given by eqns 3 and 4

	Correlation matrix				SD
	X_{ini}	$\mu_{max,0}$	$K_{X,inv}$	c_{det}	
X_{ini}					33%
$\mu_{max,0}$	0.007				16%
$K_{X,inv}$	0.003	0.87			22%
c_{det}	0.009	0.01	-0.43		14%
X_0	-0.08	-0.98	-0.90	0.12	186%

of current velocities and the temporally variable flow presumably confound the growth promoting effects of current velocity in the investigated reach of the lower Necker. The structural sensitivity analysis of the model demonstrated that a reliable identification of a mechanistic formulation of the loss process would require much more data particularly with respect to the influence of small spates on periphyton biomass (e.g. the spate of 17 March 1993). However, it also confirms that the identification of this process is independent on the process formulation.

Despite significant seasonal changes in water temperatures and daily light intensities (Fig. 1a) the influence of temperature and light on the growth rate was apparently negligible. The consideration of a temperature-dependent algal growth rate resulted in only a minor decrease in χ^2 (Table 5). Temperature

functions reported from the literature suggest changes in the relative specific growth rate ($\mu(T)/\mu_{max,0}$) by factors of 1.1–6.2 for every 10 °C increase in temperature (Bowie *et al.*, 1985). In a Sonoran desert stream post-spate recovery of the periphyton biomass (chlorophyll *a*) was about three times faster in summer than in winter indicating a significant temperature dependence of algal growth (Grimm & Fisher, 1989). On the other hand, regression analysis has often shown that only a minor fraction of the variation in periphyton biomass can be attributed to temperature (Biggs, 1988; Fisher & Grimm, 1988; Uehlinger, 1991). An apparently small temperature effect could result from seasonal changes in species composition. In the lower Necker diatoms dominate the periphyton from autumn to spring, but during summer crust forming green algae become a substantial part of the epilithic biofilm. This shift could confound the effect of the seasonal change in temperature, as diatoms have been reported to grow faster than green algae (Canale & Vogel, 1974).

Light provides the ultimate source of energy for algae and thus affects their rate of growth. However, consideration of a light function did not significantly change χ^2 . Regression analysis has shown that in streams with unpredictable flow patterns light is not a significant predictor of periphyton biomass (Fisher & Grimm, 1988; Biggs, 1988; Biggs & Close, 1989). In

Table 7 Structural sensitivity analysis of the periphyton model: Results of parameter fits. Fits are ordered with increasing number of active processes. Column 1 contains the number of the fits (the active processes can be seen in Table 4) and column 2 the χ^2 values of the original model (Equations 3 and 4 as described in ‘model description’). Columns 3–6 contain the χ^2 values of the model with alternative formulations for terms 1b and 2a

Fit	Original model	Models with an alternative formulation of term 1b or term 2a			
		Term 1b'	Term 2a'	Term 2a''	Term 2a'''
		$1 - \exp(-\ln 2 K'_{X,inv} X)$ $\ln 2 K'_{X,inv} X$	$c'_{det} Q^{3/5} (X - X_0)$	$c''_{det} Q^2 (X - X_0)$	$c'''_{det} Q (X - X_0)^2$
1	1213.9	1213.9	1213.9	1213.9	1213.9
2	1213.9	1213.9	1213.9	1213.9	1213.9
3	1213.9	1213.9	1213.9	1213.9	1213.9
4	1213.9	1213.9	1213.9	1213.9	1213.9
5	1204.7	1204.7	1084.7	1213.8	926.3
6	979.8	979.8	979.8	979.8	979.8
7	1213.9	1213.9	1213.9	1213.9	1213.9
8	1213.9	1213.9	1213.9	1213.9	1213.9
9	279.2	259.4	385.5	138.9	926.3
10	529.5	468.9	529.5	529.5	529.5
11	1204.7	1204.7	1070.0	1208.5	843.7
12	979.8	979.8	979.8	979.8	979.8
13	893.6	893.6	1068.2	1212.5	664.1
14	848.0	848.0	848.0	848.0	848.0
15	460.3	460.3	448.8	442.3	179.9
16	250.8	220.2	340.8	135.8	843.7
17	477.6	475.4	477.6	477.6	477.6
18	272.1	256.6	293.2	133.4	653.8
19	495.7	538.8	495.7	495.7	495.7
20	64.8*	64.8*	63.1*	67.6*	92.4
21	460.3	460.3	448.8	438.3	138.2
22	423.6	423.6	431.2	392.6	169.1
23	63.1*	52.8*	52.0*	67.4*	68.9*
24	64.8*	57.2*	62.7*	65.2*	86.6

* $\chi^2 < \chi^2_{0.001}$

the lower Necker the active channel (> 25 m) is too wide for light to be affected by the riparian vegetation. Therefore, autumn leave abscission has only a minor impact on light conditions at the channel surface. Light attenuation in the water column is small due the shallow channel (mean depth > 0.5 m at mean discharge). Moreover, turbidity is low except during spates. Apart from changes in the composition of the periphyton community, seasonal shifts in community structure could mask the light dependence of algal growth in the River Necker. The change in biomass is also influenced by changes in the balance between gross primary production and autotrophic respiration. Different temperature dependencies of both processes may shift this balance, and as a consequence, confound the expected light or temperature dependence of the periphyton accrual.

Mass transport limitation of nutrients into the

biofilm presumably contributes to the observed saturation of biomass accrual apart from self-shading and shear stress/drag control of the biofilm thickness. Nutrient transport into the biofilm depends on the concentration of the nutrients and the thickness of the boundary layer at the biofilm surface which is controlled by flow-induced turbulence. In the Necker, where concentrations of inorganic phosphorus and nitrogen compounds are rather high (Table 2), the model predicts a change from exponential to linear growth when chlorophyll *a* exceeds about 15 mg m⁻² (half saturation concentration $1/K_{X,inv}$; fit 20 in Table 4). Studying the diatom accrual in troughs Bothwell (1989) found exponential growth up to a biomass of 30 mg Chl *a* m⁻², although nutrient concentrations were distinctly lower ($\approx 0.6 \mu\text{g SRP l}^{-1}$) than in the Necker. The use of a biomass-limited growth term may allow the model to be used in streams which

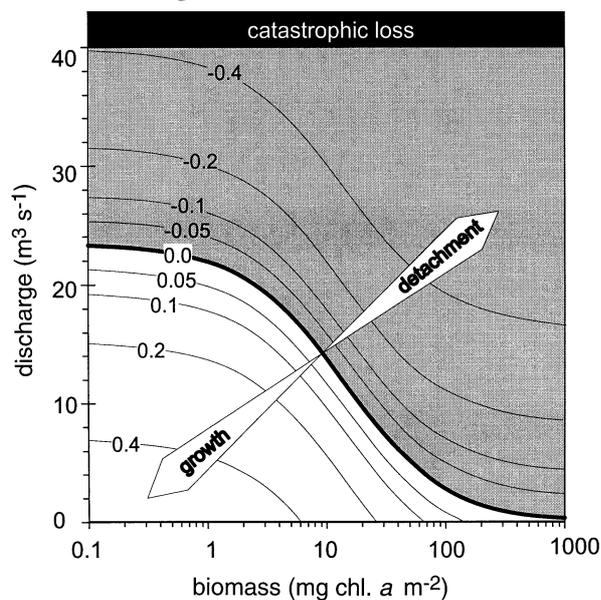


Fig. 4 Net specific rate of change of chlorophyll a $k = \frac{1}{X} \frac{dX}{dt}$ (contours) as a function of chlorophyll a (mg Chl a m^{-2}) and discharge ($m^3 s^{-1}$). The hatched area delimits the area of flow-induced net biomass detachment.

differ with respect to the supply of nutrients, as long as the supply of nutrients is not subject to significant seasonal variation. However, the recalibration of the model would be necessary in order to adjust $K_{X,inv}$ (term 1b) to each nutrient supply regime. Flume experiments show that nutrient additions to water with low ambient nutrient concentrations increase the accrual rate of periphyton on bare substrata (Horner *et al.*, 1983, 1990; Triska *et al.*, 1983; Grimm & Fisher, 1986; Bothwell, 1989; Guasch, Martí & Sabater, 1995). Therefore, the time required to restore pre-spate biomass is expected to decrease with increasing nutrient supply (Grimm & Fisher, 1986). On the other hand Mulholland *et al.* (1991) found that low nutrient supply did not result in low periphyton accrual after experimental scour disturbance. There is some evidence that rapid biomass-specific nutrient recycling may allow relatively high accrual rates of periphyton in spite of low nutrient inputs (Mulholland *et al.*, 1991; Paul, Duthie & Taylor, 1991).

Several studies indicate that primary consumers are able to influence the algal abundance in streams (e.g. Lamberti & Resh, 1983; Jacoby, 1987; Dudley & D'Antonio, 1991). If grazer populations suffer severe loss by bed moving spates, grazing is thought to become effective only during later stages of the succes-

sion of the periphyton community, because generation times of algae are short compared with those of grazers (Power, 1992). However, observations and field experiments indicate that in the lower Necker the impact of moving bed sediments on grazing invertebrates is relatively small or temporally limited (Uehlinger & Meyer, 1992; Matthaei *et al.*, 1996). On the other hand consumption rates may be small compared with nutrient-saturated growth rates. Unfortunately, there was no information on invertebrates for the period during which periphyton was sampled to test this hypothesis.

In the River Necker, as in other streams, the distribution of periphyton is very patchy (McConnell & Sigler, 1959; Tett *et al.*, 1978; Fisher *et al.*, 1982; Uehlinger, 1991). This patchiness results from local differences in depth, current velocity, availability of light and the stability of the substratum (McConnell & Sigler, 1959; Tett *et al.*, 1978; Uehlinger, 1991; Biggs & Stokseth, 1996). The shear stress necessary to initiate motion of a particle depends not only on the size of the particle but also on the size of neighbouring particles (Andrews, 1983). Moreover, the predictability of succession sequences of periphyton in disturbed patches may be low (Fisher, 1983, 1990). All this results in a rather undeterministic mosaic of periphyton patches. Such small-scale heterogeneities are smoothed by focusing the interest on a reach of 2 km length. At this larger scale the periphyton biomass recovers along rather deterministic trajectories.

The modified McIntire model allows the simulation of periphyton dynamics on a spatial scale which corresponds to that under which measurements of the ecosystem metabolism are usually made. Its application to rivers with similar disturbance regimes requires estimates of the system specific detachment function and the critical discharge for disruption of the sediment surface, which both depend on the shape of the channel cross-section, channel slope, size distribution and spatial structure of the uppermost bed sediments. It also requires adjustment of growth rates to allow for different nutrient loadings. In a river with an unpredictable disturbance regime, such as the Necker, an 18-month periphyton record seems to be a minimum for the reliable identification of model processes.

The results of this investigation are basically the same as those of multiple stepwise regression analysis. Both methods show the importance of flow-related parameters for the control of periphyton dynamics

and in both models periphyton biomass is hardly dependent on temperature and light. The present study is an attempt at modelling periphyton biomass in a real stream and it incorporates catastrophic loss by spates. In contrast to regression models the dynamic model used in this approach has the potential to lose its empirical character through future refinements and adequate sampling.

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