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Assessing the importance of a self-generated detachment process in river biofilm models

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SUMMARY

1. Epilithic biofilm biomass was measured for 14 months in two sites, located up- and downstream of the city of Toulouse in the Garonne River (south-west France). Periodical sampling provided a biomass data set to compare with simulations from the model of Uehlinger, Bürher and Reichert (1996: *Freshwater Biology*, **36**, 249–263.), in order to evaluate the impact of hydraulic disturbance.

2. Despite differences in application conditions (e.g. river size, discharge, frequency of disturbance), the base equation satisfactorily predicted biomass between low and high water periods of the year, suggesting that the flood disturbance regime may be considered a universal mechanism controlling periphyton biomass.

3. However modelling gave no agreement with biomass dynamics during the 7-month long low water period that the river experienced. The influence of other biomass-regulating factors (temperature, light and soluble reactive phosphorus) on temporal biomass dynamics was weak.

4. Implementing a supplementary mechanism corresponding to a temperature-dependent self-generated loss because of heterotrophic processes allowed us to accurately reproduce the observed pattern: a succession of two peaks. This case study suggests that during typical summer low water periods (flow stability and favourable temperature) river biofilm modelling requires self-generated detachment to be considered.

Keywords: autogenic sloughing, biomass dynamics, detachment, epilithic biofilm, river model

Introduction

As a zone of transient storage, epilithic biofilms influence biogeochemical processes in shallow streams (Battin *et al.*, 2003), especially nitrogen cycling (Teissier *et al.*, 2002). Nutrient concentrations and flow disturbance are considered the major external driving variables influencing periphyton colonisation, growth, immigration and removal processes (Biggs & Close, 1989; Lohman, Jones & Perkins, 1992; Chételat *et al.*, 1999). A modelling approach has been extensively employed as a convenient tool to identify the factors

that primarily control temporal variability in epilithic biomass and several models are available for head-water streams (Horner, Welch & Veenstra, 1983; Uehlinger *et al.*, 1996; Saravia, Momo & Boffi Lissin, 1998; Asaeda & Hong Son, 2000). Modelling detachment processes in natural river biofilm assemblages mainly focuses on the response of the periphyton community as a function of hydraulic forces (discharge, velocity of water flow and roughness of the substrata). Non-flow mediated detachment sources are assumed to be constant or are simply included in a net growth term because their minor impact cannot be detected in studies where flow-mediated detachment dominates over decay processes. In less unpredictable flow regimes involving other kinds of microbial biofilms (e.g. in biofilm airlift suspension reactors) other detachment mechanisms (erosion, abrasion and

sloughing) have been more precisely investigated using experimentation or modelling (Morgenroth & Wilderer, 2000; Telgmann, Horn & Morgenroth, 2004).

In rivers with extended periods of low flow, the dynamics of epilithic biomass are expected also to depend on self-generated detachment. This hypothesis was tested with an adapted version of a dynamic periphyton model previously proposed by Uehlinger *et al.* (1996). Simulated biomasses were compared with a biomass data set collected in a large French river (Garonne River). We particularly focused on epilithic biomass dynamics during an unusually long low water period; by implementing a new equation we checked for the impact of autogenic sloughing in the absence of hydraulic disturbances. The possible influence of other allogenic factors (temperature, light and nutrient availability) was first investigated to test for their respective influence on simulated biomasses.

Methods

Study site

The Garonne River (south-west France) is a large river (eighth order, 600 km long) with pebble banks covered by epilithic biofilm even in channels up to the seventh order. Study sites were located 36 km upstream (upstream site, sixth order) and 12 km downstream (downstream site, seventh order) of Toulouse, an urban centre with 965 000 inhabitants. The mean daily discharge at Toulouse is $200 \text{ m}^3 \text{ s}^{-1}$ (minimum $30 \text{ m}^3 \text{ s}^{-1}$ to maximum $3500 \text{ m}^3 \text{ s}^{-1}$). During the low water period (from July to October), the mean discharge is about $50 \text{ m}^3 \text{ s}^{-1}$ and the river is characterised by a shallow (<1.5 m) and wide bed (100 m) with a mean water velocity on the riverbed of 0.5 m s^{-1} . Low turbidity (<30 NTU) favours the development of epilithic biomass. According to Eulin & Le Cohu (1998), epilithic algal communities are dominated by typical diatoms of a moderately mineralised river of a limestone region, most species being rheophile and alkaliphile.

Sampling procedure and biomass measurement

Sampling was performed from July 2001 to December 2001 at weekly intervals and then monthly until November 2002. The sampling strategy was designed

to ensure that sample collection was as repeatable and as regular as possible. Note that collection of pebbles on the riverbed was only possible when discharge was lower than $200 \text{ m}^3 \text{ s}^{-1}$. For each study site, a reference point was chosen in a riffle. At this reference point, sampling was performed on each date at three distinct depths of the cross section: 30, 50 and 70 cm. Three pebbles (mean diameter: 12 cm) from each depth were collected and depth samples were pooled for biomass analysis. Within 6 h of collection, biofilm was removed from the upper surface with a toothbrush and suspended in filtered water ($0.2 \mu\text{m}$). The scrubbed surface of the pebbles was traced on tracing paper and its area (m^2) calculated from the mass of the tracings. Biomass records of the three depths were then averaged to provide a mean \pm SE biomass data for each date at each site. According to the results of a previous study the recorded biomass is not representative of the biomass occurring at all points of the cross section (e.g. the tidal zone close to the banks and at maximum depth) but satisfactorily describes the low depth region of the cross section where epilithic biofilm typically develops (Améziane *et al.*, 2002). In the Garonne River such biomass records may thus be representative of the epilithon dynamics of this kind of river bottom facies.

Dry mass (DM) was obtained by weighting the dry pellet ($80 \text{ }^\circ\text{C}$, overnight) after centrifugation (2300 g, 20 min) of a 50 mL aliquot of biofilm suspension. The dry pellet was combusted ($500 \text{ }^\circ\text{C}$, overnight) and weighed to determine ash-free dry mass (AFDM). A second aliquot (10 mL) of the bio-film suspension was centrifuged (12 000 g, 20 min, $4 \text{ }^\circ\text{C}$). The chlorophyll *a* content was measured spectrophotometrically using trichromatic equations (Jeffrey, Mantoura & Wright, 1997) after extraction with acetone 90% (4 h, darkness, room temperature) of the suspended (tissue homogeniser) and ground (ultrasonic disintegrator) pellet.

Environmental variables

Mean daily discharges were supplied by three gauging stations of the French water management authorities (DIREN Midi-Pyrénées). The gauging station at Portet-sur-Garonne provided daily discharge records for the upstream site after subtraction of the Ariège tributary mean daily discharge recorded at the gauging station at Auterive. The station of

Verdun-sur-Garonne provided discharge records for the downstream site. The French meteorological society (Météo France) provided global daily radiation at Lherm (20 km on south-west from Toulouse). Each global daily radiation (J cm^{-2}) was first converted to daily integrated photosynthetically (400–700 nm) active radiation I (J cm^{-2}) according to Steemann-Nielsen (1975). To compare with Uehlinger *et al.* (1996), I was converted as a photon flux density expressed as E m^{-2} (equivalent to mol m^{-2}). Mean daily water temperatures were calculated from hourly temperatures supplied by DIREN Midi-Pyrénées. Water soluble reactive phosphorus (SRP), ammonium, nitrite and nitrate concentrations were quantified by standard colorimetric methods [American Public Health Association (APHA), 1992] from filtered water samples collected at each biomass sampling campaign.

Modelling approach

Initial model. We used the structure of the differential equation developed by Uehlinger *et al.* (1996) for a Swiss prealpine gravel bed river characterised by unpredictable and frequent disturbances. Two terms compose the differential equation of epilithic biomass B (g AFDM m^{-2}) in accordance with the benthic algal theoretical curve proposed by Biggs (1996): an accrual term and a loss term.

$$\frac{dB}{dt} = \mu_{\max} B \frac{1}{1 + k_{\text{inv},B} B} \frac{I}{k_I + I} e^{\beta(T-T_0)} - c_{\text{det}} Q (B - B_0) \quad (1)$$

The accrual term is mainly based on a net biomass growth term (μ_{\max}) limited by biomass thickness ($k_{\text{inv},B}$). The biofilm thickness is considered as a variable of growth limitation; in a biofilm mat of increasing thickness, the surface layers are supported by better light (and nutrient conditions) than deeper layers. A detachment term directly proportional to the mean daily discharge Q and to biomass B composed the loss term (c_{det}).

Two other growth limitation terms $I/(k_I + I)$ and $e^{\beta(T-T_0)}$ account for the influence of seasonal variations in light (k_I) and temperature (β and T_0) on the growth rate. The reference temperature T_0 was set to 20 °C.

We decided to remove from (1) the catastrophic loss term proposed by Uehlinger *et al.* (1996) and activated

when discharge is higher than a critical discharge. Its impact on epilithic biomass was short term and did not give significant changes.

Model development: SRP impact. Water SRP concentrations (k_P) were included in the equation to complete the set of external factors.

$$\frac{dB}{dt} = \mu_{\max} B \frac{1}{1 + k_{\text{inv},B} B} \frac{[\text{SRP}]}{k_P + [\text{SRP}]} - c_{\text{det}} Q (B - B_0) \quad (2)$$

The growth rate nutrient limitation term is the classic Monod function widely used to represent SRP limitation of algal growth in freshwater systems. The Monod function assumes that the growth rate of periphyton increases rapidly with P at low concentrations of SRP and becomes insignificant at high P concentrations.

Model development: self-generated detachment. Self-generated detachment is a sizeable and rather sudden loss of biofilm standing stock that can arise because of a decrease of attached biomass resistance to floating and drifting. This occurs when the biofilm becomes thicker and less cohesive. Senescence of the deeper algal layers, their heterotrophic degradation and consequent respiratory gas bubble production is the typical autogenic sequence that results in sloughing of a mature biofilm. Various maturation-related processes such as enhanced meiofauna activity may also contribute to self detachment, which may thus be schematically viewed as a shift from photoautotrophic accrual to heterotrophic losses.

Self-generated detachment was assumed to be mainly triggered by the bacterial degradation of the biofilm mat, which is in turn strongly controlled by temperature. A self-generated detachment term (c_{auto}) is a conceptual formulation indicating that favourable temperature conditions may activate bacteria involved in the degradation process and hence emphasise sloughing.

This term was formulated using the same form as the discharge-dependant term of Uehlinger *et al.* (1996): lost epilithic biomass is an increasing function of biomass of biofilm standing stock, thus proportional to $(B - B_0)$. Loss is thus expressed as a function of the active bacterial density B_b (cells m^{-2}).

$$\frac{dB}{dt} = \mu_{\max} B \frac{1}{1 + k_{\text{inv},B} B} - c_{\text{det}} Q(B - B_0) - c_{\text{auto}} B b(B - B_0) \quad (3)$$

The active bacterial density Bb was simultaneously described by a simple differential equation composed by a growth and a loss term.

$$\frac{dBb}{dt} = [\mu_{Bb} e^{\beta_{Bb}(T - T_{0Bb})} - c'_{\text{det}} B] Bb \quad (4)$$

Active bacterial density accrual was approximated by a temperature limited growth rate; temperature limitation was expressed by the Arrhenius or van't Hoff equation [β_{Bb} and T_{0Bb} , the reference (optimal) temperature]. The loss term (c'_{det}) was expressed as a detachment term considering that biofilm detachment (discharge-dependant and/or self-generated) simultaneously causes bacterial matter losses. Epilithic biomass B was thus chosen as an integrative variable explaining bacterial detachment. Other kinds of loss (death, lysis) were included in μ_{Bb} . The list of parameters symbols, units and names was detailed in Table 1.

Model resolution, calibration and settings. Equations were resolved using the Runge-Kutta method (fourth order). Preliminary tests had demonstrated the accuracy of a time step fixed at 3 h. Values of discharge, temperature, light and SRP at each time step were obtained by linear interpolation of observational data.

Table 1 Model parameters

Symbols	Units	Names
First equation		
μ_{\max}	d^{-1}	maximum specific growth rate
$k_{\text{inv},B}$	$\text{g AFDM}^{-1} \text{m}^2$	inverse half-saturation constant
k_l	E m^{-2}	light half-saturation coefficient
β	$^{\circ}\text{C}^{-1}$	coefficient of temperature
T_0	$^{\circ}\text{C}$	reference temperature (20 $^{\circ}\text{C}$)
k_p	$\text{mg}^{-1} \text{L}$	phosphorus half-saturation constant
c_{det}	$\text{s m}^{-3} \text{d}^{-1}$	detachment coefficient
B_0	g AFDM m^{-2}	minimal biomass
c_{auto}	$\text{cells}^{-1} \text{m}^2$	self-generated detachment coefficient
Second equation		
μ_{Bb}	d^{-1}	maximum specific growth rate
β_{Bb}	$^{\circ}\text{C}^{-1}$	coefficient of temperature
T_{0Bb}	$^{\circ}\text{C}$	reference temperature (20 $^{\circ}\text{C}$)
c'_{det}	d^{-1}	bacterial detachment coefficient

Model simulations and parameter estimation in the eqns (1) and (2) were based on the minimisation of chi-square in each site. The initial value of epilithic biomass B was fixed at 4 g AFDM m^{-2} in accordance with average initial measured biomasses in both sites. The initial Bb value was fixed in accordance with previous studies showing that epilithic bacterial densities represented on average 3×10^{10} cells (g AFDM) $^{-1}$ (Lyautey *et al.*, 2003, 2005a). The initial Bb value was thus equal to 1×10^{11} cells m^{-2} in accordance with the retained initial B value.

Results

Environmental variables and biomass dynamics

Active radiation I exhibited a typical seasonal cycle between an irradiance of 63 E m^{-2} in summer to 2 E m^{-2} in winter (Fig. 1a). Water temperature described a parallel pattern, varying between 27 $^{\circ}\text{C}$ in August and 0.5 $^{\circ}\text{C}$ in December (Fig. 1b). During the modelling period (July 2001 to November 2002), the Garonne River exhibited stable hydrology with a mean flow of 60 $\text{m}^3 \text{s}^{-1}$ (minimum 35 to maximum 225) from July 2001 to January 2002 followed by a disturbed hydrological period with a mean flow of 182 $\text{m}^3 \text{s}^{-1}$ (maximum 1183 $\text{m}^3 \text{s}^{-1}$ to minimum 45 $\text{m}^3 \text{s}^{-1}$) from February to November 2002 (Fig. 1c). Our study period began on 19 July 2001 after 6 months of high water that initialised the growth biofilm. SRP concentrations were quite stable with an average of 9 $\mu\text{g L}^{-1}$ in the upstream site (Fig. 1d). In the downstream site, SRP concentrations were more variable around an average of 100 $\mu\text{g L}^{-1}$. Mean (\pm SE) N/P ratios were 29 (\pm 4.8) and 14 (\pm 0.6) for the upstream and downstream sites respectively.

Epilithic biomass was estimated using three area-specific masses, namely DM, AFDM and chlorophyll a per square meter (Fig. 2). Irrespective of the method used to estimate biomass, epilithic biomass exhibited the same pattern at both sites: two successive peaks of biomass, occurring in summer (from July 2001 to November 2002) and in winter (from November to March 2002). In summer, biomass reached a maximum of 156 and 151 g DM m^{-2} (in upstream and downstream sites, respectively), 24 and 25 g AFDM m^{-2} , 146 and 115 mg chlorophyll $a \text{ m}^{-2}$. In winter, biomass reached a maximum of 217 and 157 g DM m^{-2} (in upstream and downstream sites, respectively), 30 and

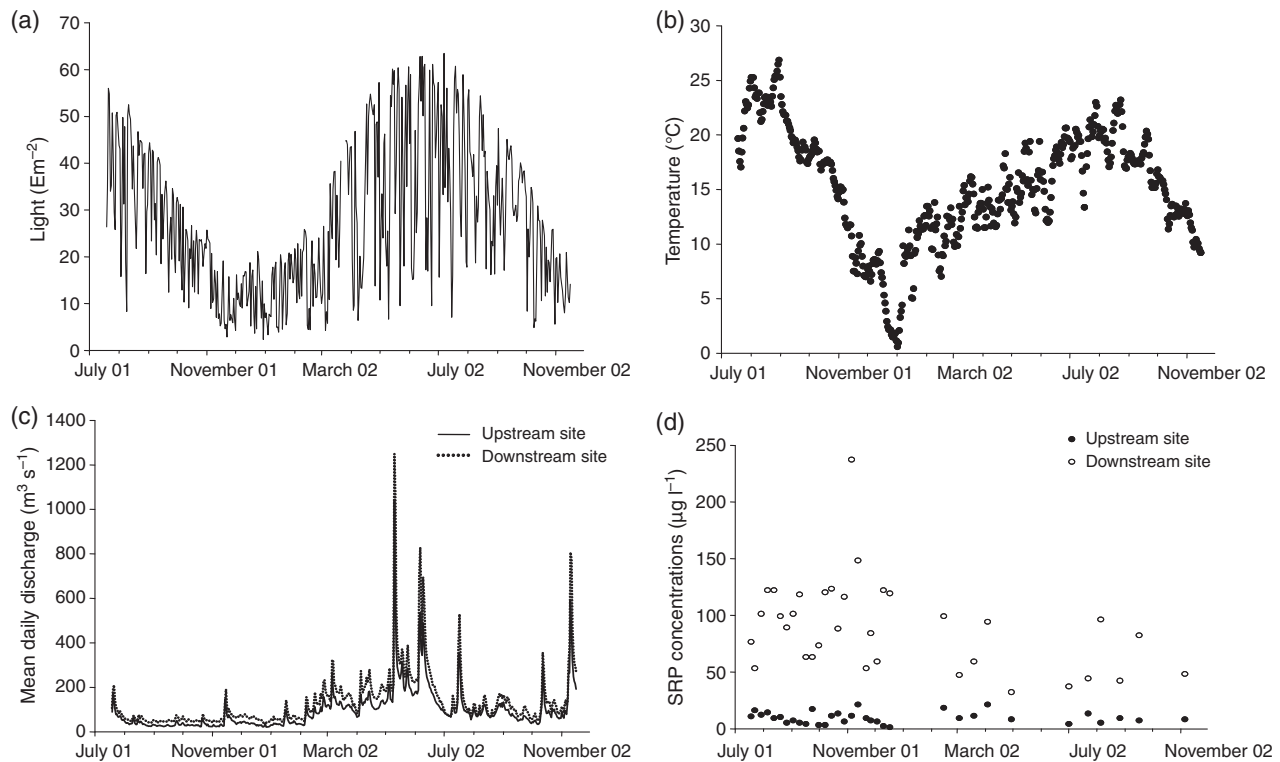


Fig. 1 Seasonal changes in (a) light, (b) temperature, (c) mean daily water discharge and (d) SRP concentration from July 2001 to November 2002 in the upstream and downstream sites.

29 g AFDM m^{-2} , 282 and 195 mg chlorophyll *a* m^{-2} . DM and AFDM ($r^2 = 0.80$, $n = 66$, $P < 0.001$) and chlorophyll *a* and AFDM ($r^2 = 0.61$, $n = 59$, $P < 0.001$) were significantly correlated in the two sites. The weaker correlation found between chlorophyll *a* and AFDM could be related to chlorophyll *a* cell content, which increases with decreasing light intensity in winter (data not shown). Pigment chromatic adaptation (to low light particularly) may alter the ratio between these chemical indicators.

Initial model

The first simulation combining the net growth term limited by biomass thickness and discharge (Fig. 3a,b) provided satisfactory levels of epilithic biomass as indicated by the chi-square drop when discharge detachment was activated (Table 2; fits U2 and D2). As measured by chi-square value, model calibration seemed to provide a better fit in the upstream site. In both sites, however, modelling reproduced global differences in biomass values in relation to mean flow. Conversely, during the 7-month low water period,

simulations did not reproduce intermediary biomass losses and showed poor agreement with measured data in both sites, especially between September 2001 and January 2002 when measured epilithic biomass was decreasing.

Light and temperature limitation terms did not improve simulations, particularly during the first low water period (Fig. 3c,d; Table 2; fits U3, D3, U4 and D4). Conversely, because of the substantial reduction in I (from 26 to 5 $E m^{-2}$; Fig. 1a) and temperature (from 25 to 1 °C; Fig. 1b) from November 2001 to January 2002, the biomass simulated with overstated temperature and light parameters decreased while the measured biomass values continued to increase.

SRP impact

The introduction of an SRP limitation term did not substantially improve the fit with observed data (Table 2; fits U5 and D5). The influence of SRP limitation on epilithic biofilm accrual rate differed between the sites (Fig. 3e,f), as expected given differences in their SRP levels. The term was negligible in

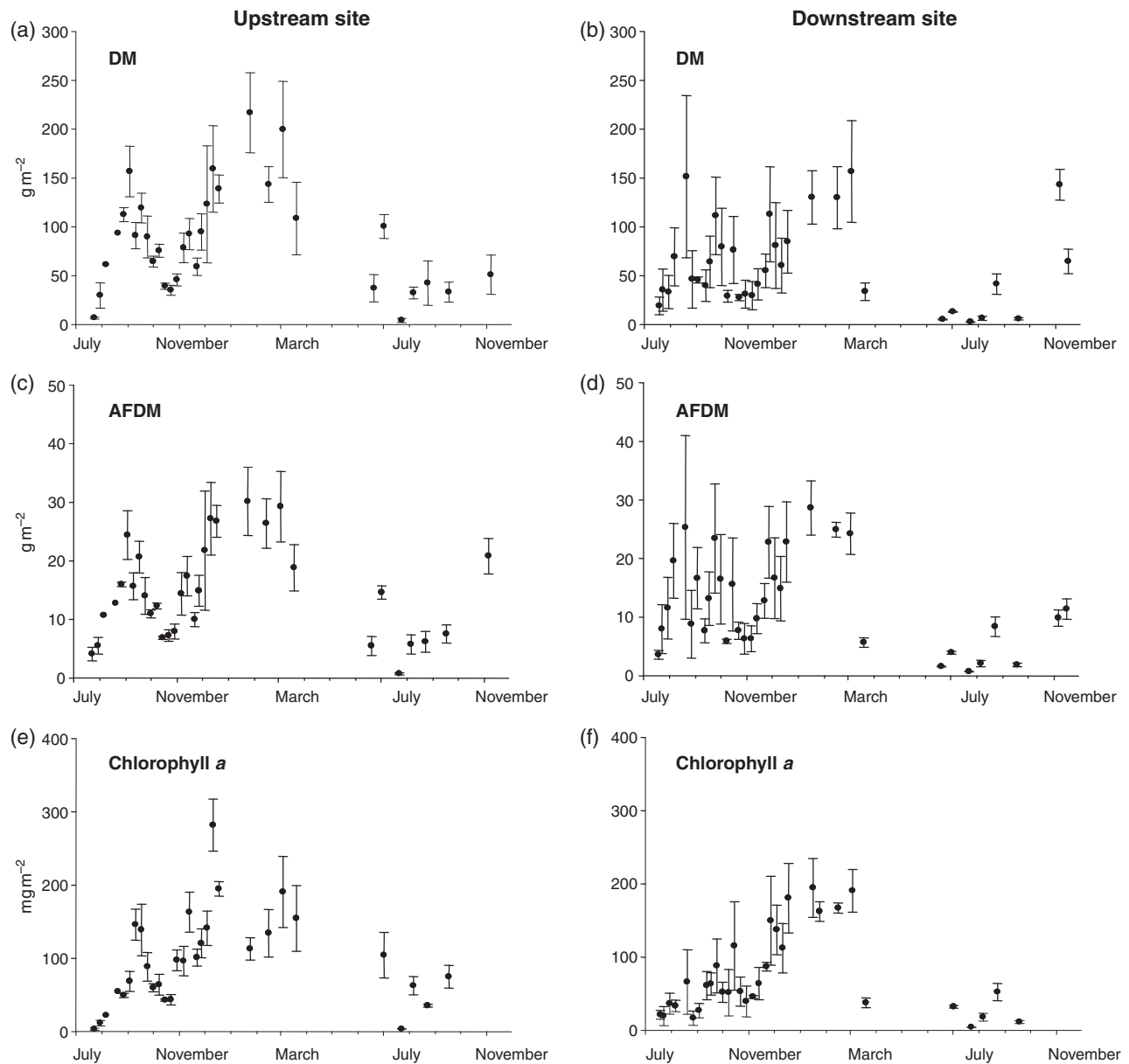


Fig. 2 Biofilm dynamics (mean \pm SE) expressed as (a,b) dry mass DM, (c,d) ash-free dry mass AFDM and (e,f) chlorophyll *a* from July 2001 to November 2002 in the upstream and downstream sites.

determining the accrual rate in the downstream site but was responsible for a substantial reduction in the upstream site.

Self-generated detachment

The addition of a self-generated sloughing term allowed the model to reproduce the decrease of epilithic biomass in September 2001 at both sites (Fig. 3g,h). This resulted in substantial change

of chi-square values in the upstream and downstream sites (Table 2; fits U8 and D8). A loss was generated from July 2001 to January 2002, increasing to more than $1\ g\ AFDM\ m^{-2}$ in the upstream site and to $0.5\ g\ AFDM\ m^{-2}$ in the downstream site (Fig. 4a,b). Note that the implementation of the self-generated detachment term only improved the initial model considering as long as it was considered to be a supplement to a flow-mediated loss (Table 2; fits U9 and D9). Deactivation of bacterial detachment ($c'_{det} = 0$) or

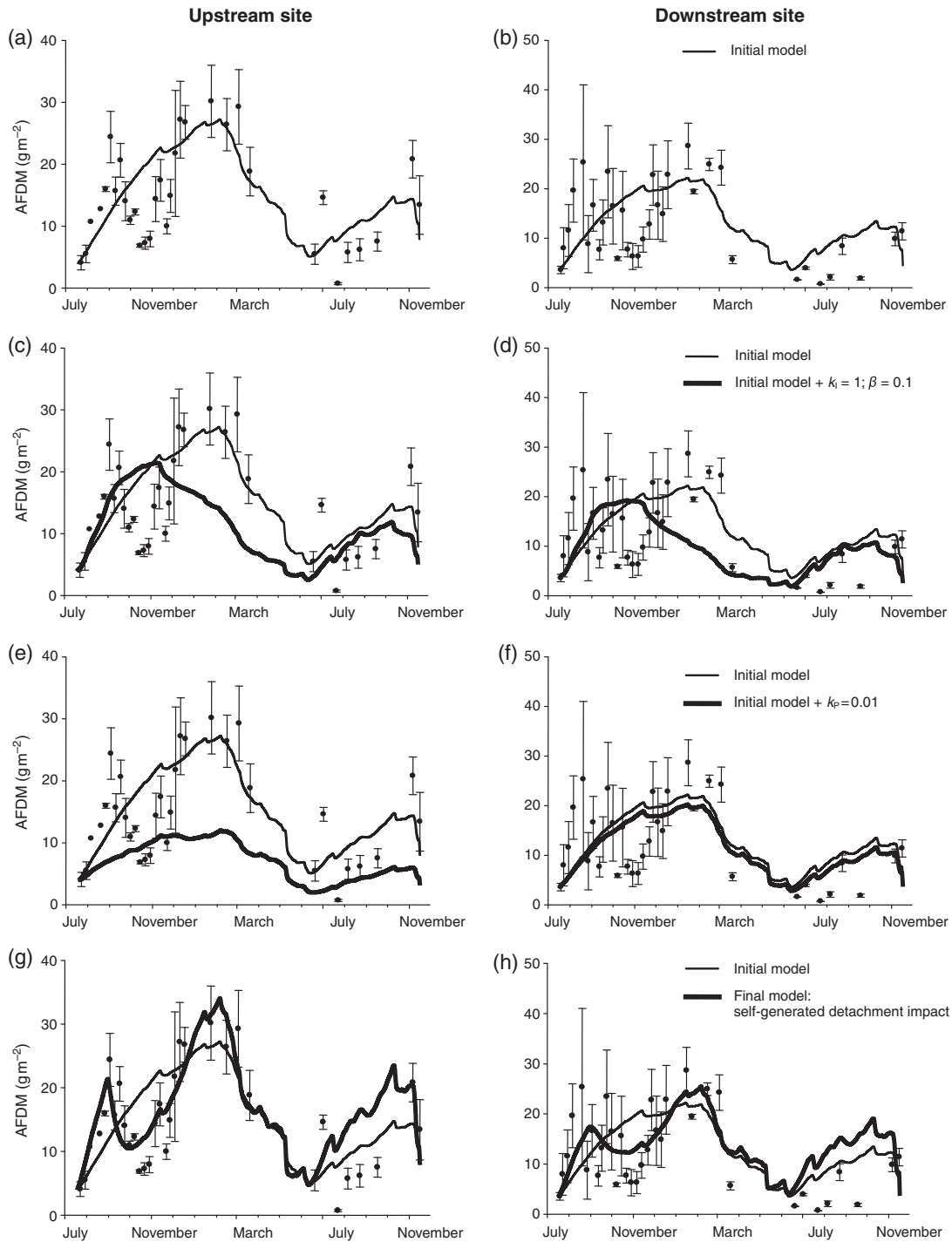


Fig. 3 Model simulations: biofilm ash-free dry mass (g AFDM m^{-2}). Comparisons between measured (mean \pm SE) and simulated biomasses (lines) from July 2001 to November 2002 in the upstream site and the downstream site. (a, b) Initial models. Represented simulation corresponds to the fits U2 and D2 in Table 2; (c, d) Light and temperature impact on initial models; (e, f) SRP impact on initial models; (g, h) Final models: self-generated detachment. Represented simulations correspond to the fits U2, D2, U8 and D8 in Table 2.

Table 2 Result of parameter fits (minimisation chi-square) of the model simulations. The fits are ordered with different active processes. Bold and narrow text respectively corresponds to simulations in the upstream (U) and the downstream (D) sites. Each number marks the value of the parameter. Empty cells mark the parameters set to zero and not included in the fit.

Fit	Accrual					Loss							χ^2 -value
	Biofilm thickness limited		Light limited k_1	Temperature limited β	SRP limited k_P	Discharge-dependant			Self-generated				
	μ_{\max}	$k_{\text{inv},B}$				c_{det}	B_0	c_{auto}	μ_{Bb}	c'_{det}	β_{Bb}		
U1	6.64	10.5											268.1
D1	13.12	25.4											386.3
U2	7.84	3.8				0.0016	0.00001						88.1
D2	25.28	10.9				0.0016	0.00001						136.7
U3	7.28	3.5	0.001			0.0016	0.00001						88.1
D3	25.28	10.9	0.001			0.0016	0.00001						136.7
U4	7.28	3.5		0.00001		0.0016	0.00001						88.1
D4	25.28	10.9		0.00001		0.0016	0.00001						136.7
U5	7.36	3.5			0.0001	0.0016	0.00001						88.1
D5	26.16	11.0			0.002	0.0016	0.00001						136.1
U6	20.00	9.6				0.0016	0.00001	3×10^{-15}	0.0008				87.6
D6	57.6	23.9				0.0016	0.00001	4×10^{-15}	0.040				135.6
U7	20.80	9.0				0.0016	0.00001	9×10^{-15}	0.80	0.056			75.1
D7	72.8	22.9				0.0016	0.00001	3×10^{-14}	0.768	0.0552			119.9
U8	5.52	1.0				0.0032	0.00001	5×10^{-17}	0.176	0.0216	0.60		55.6
D8	61.6	13.9				0.0024	0.00001	5×10^{-16}	0.688	0.384	0.23		102.1
U9	26.16	13.6						2×10^{-15}	0.080	0.000008	0.53		122.0
D9	44.32	15.0						2×10^{-15}	0.080	0.000008	0.57		151.4

temperature limitation ($\beta_{Bb} = 0$) gave poorer agreement with measured data (Fig. 4c,d), indicating that the employed parameters were appropriate. A Bb loss term (represented by c'_{det}) was necessary to balance Bb growth (deactivation of c'_{det}). Comparisons between the final simulation and the deactivated β_{Bb} simulation indicate that temperature sensitivity may explain the first biomass peak.

Discussion

Initial model

The model developed by Uehlinger *et al.* (1996) was based on the hypothesis that disturbances produced by spates are the major mechanism controlling periphyton biomass in streams, initiating new cycles of accrual, metabolic and structural succession (Biggs & Thomsen, 1995). This convenient model has been retained in our study because the variables were easy to measure, parameters are explicit and calibration and validation have been performed with a long-term measured data set. However, we preferred to assess

biomass dynamics using AFDM, which describes the entire biomass of the biofilm assemblage, rather than chlorophyll *a*, which only relates to the algal part of the mat and can be subject to changes because of photoadaptation.

Some differences in conditions can be listed between the present study and that of Uehlinger *et al.* (1996): mean annual discharge (200 versus $4.6 \text{ m}^3 \text{ s}^{-1}$), river width (80 versus 25 m) and disturbance frequency (one flow event per 2 months versus one flow event per 2 weeks). Despite these differences, the equation combining growth, nutrient limitation and a light diffusion term, together with loss related to a discharge effect, simulated satisfactory levels of biomass during annual low and high water periods. The mean seasonal epilithic biomass in the Garonne River is thus likely to be controlled by hydrological disturbance intensity in accordance with previous studies showing that more than 60% of the variance in periphyton biomass in streams can be explained by spates (Biggs & Close, 1989; Uehlinger *et al.*, 1996). By activating light and temperature limitation terms in our model we found that neither active radiation nor

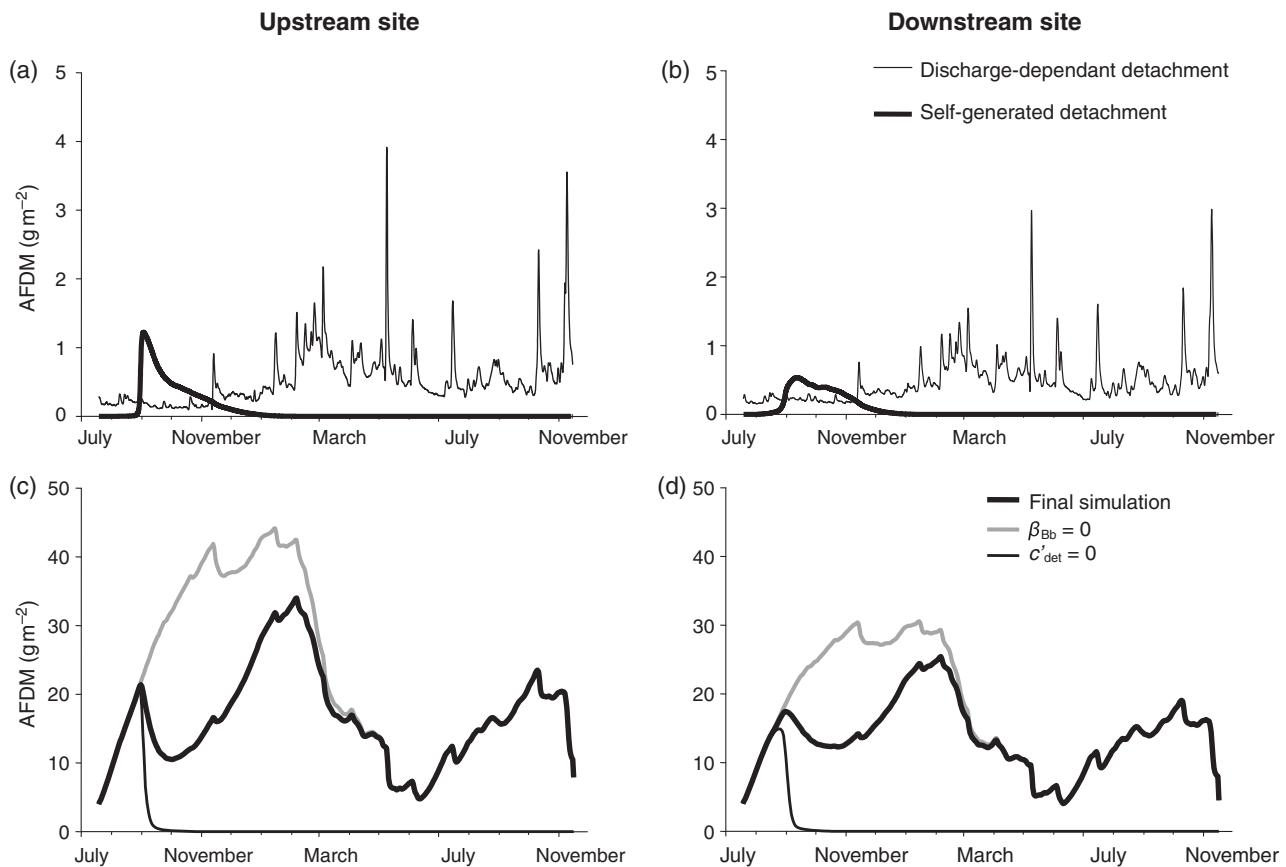


Fig. 4 (a, b) Temporal dynamics of losses because of self-generated detachment (bold line) and discharge-dependant detachment (thin line) from July 2001 to November 2002 in the upstream and downstream sites. (c, d) Response of epilithic biomass to deactivation of temperature ($\beta_{Bb} = 0$) and loss ($c'_{det} = 0$) parameters from July 2001 to November 2002 in the upstream and downstream sites.

water temperature improved the simulation of biomass dynamics at the observed seasonal scale. Despite a seasonal decrease of water temperature and light, comparable biomass values were reached in both epilithon peaks (about 30 g AFDM m^{-2}), suggesting that within this range of variation neither light nor temperature had a substantial effect. Moreover, three out of the five algal species accounting for nearly 80% of algal biomass were common to both peaks (J. Brabet & L. Ten Hage, unpublished data): *Diatoma vulgare* Bory, *Melosira varians* Agardh and *Amphora ovalis* Kütz, indicating that a few taxa, quite well adapted to temperature seasonal changes, may have sustained epilithic biomass development.

SRP impact

Nutrient availability is an important factor influencing periphyton development in streams, particularly dur-

ing periods without spates (Biggs, 1995). Taking into account the recorded biomass, the sampled sections of the Garonne River can be considered to be 'enriched' according to Biggs (1996), or 'eutrophic' according to Dodds, Jones & Welch (1998). It thus seems that no nutrient deprivation occurred in the biofilms, as compared with the river sampled by Uehlinger *et al.* (1996). The N/P ratios in each site indicate that SRP would be the less available element in this system. As expected, implementing a SRP limitation term during these periods did not improve the simulation of biomass temporal variations but accurately simulated differences in epilithic biomass accrual rates between sites. The impact of urban discharges on epilithic community structure or activity had previously been evidenced in the Garonne River (Teissier *et al.*, 2002; Lyautey *et al.*, 2003). Differences in epilithic biomass accrual rates between sites might thus be due to changes in nutrient loads.

Self-generated detachment impact

Uehlinger *et al.* (1996) included in the net growth rate μ_{\max} other implicit loss factors (decay, loss by grazing and discharge-independent detachment). Nevertheless floods were so frequent and intense that biomass growth curves were periodically truncated by spates and that impact of other loss terms were negligible. Algal communities in streams exhibiting frequent floods tend to have the characteristics of immature or pioneer communities (Odum, 1969; Biggs, Stevenson & Lowe, 1998) as the maturation of the epilithic biomass and thus community succession, is truncated. In such cases, colonisation and rapid growth are the distinctive characters of the communities and accrual is the dominant process. Modelling net phototrophic growth is then satisfactory to simulate epilithic biomass dynamics. This may explain why the direct application of Uehlinger's model simulated adequate levels of biomass during one hydrological cycle in any given hydrosystem. According to the theoretical benthic algal growth curve proposed by Biggs (1996), when no hydrological disturbance occurs, an accrual phase because of immigration/colonisation is followed by losses through a combination of death, emigration, sloughing and removal by grazing. Epilithic biomass removal by autogenic sloughing and grazing typically occurs with increasing time since the last disturbance (Leff *et al.*, 1994; Biggs, 1996; Lawrence *et al.*, 2002; Battin *et al.*, 2003). Decreasing of the resistance of benthic algae with community age and biomass may favour autogenic sloughing (Peterson, Hoagland & Stevenson, 1990). Grazing may also be a relevant constraint after a long period without spates since the recovery of invertebrates is usually slow compared with periphyton growth (Biggs & Close, 1989).

In our study sites, an analysis of the epilithic community structure in relation to abiotic factors has been performed by Lyautey *et al.* (2005b). This showed that recorded biomass dynamics (July 2001 to March 2002) may not have simply represented a single production event interrupted by disturbance, but rather a sequence of two production events with accrual and loss phases. Typical life history and diet parameters of benthic invertebrates (e.g. Benke, 1979; Basaguren, Riano & Pozo, 2002) suggest that the studied period (July to December) should be characterised by high numbers of small individuals which have lower energetic demands. Ingestion by inverte-

brates should thus have been low and rather constant. Subsequent losses because of grazing were unlikely to occur during the loss phase. We assumed therefore that epilithic biomass underwent autogenic evolution. Indeed hydrological stability, seasonal variations of light and temperature and biofilm accrual were the main variables that might have driven bacterial community succession. As hydrological, chemical and biological data supported the hypothesis of an autogenic evolution of epilithic biomass within each production event, autogenic sloughing was considered to be a function of resource stress of underlying layers, because of bacterial activity indicated by the intensification of the heterotrophic decay processes in the course of biofilm maturation. Our model, including a new detachment term, provided a good simulation of epilithic biomass during the low water period, supporting the hypothesis that the dynamics of mature epilithic biomass are not only driven by photoautotrophic growth but also by a heterotrophic loss process.

As already mentioned, temperature is unlikely to have affected the extent of biomass accrual. Changes in temperature could nevertheless explain differences between the first and the second production events; in particular, the limitation of bacterial activity by low temperature might have led to the stability of the second peak of biomass. The time taken to reach the first epilithic biomass peak (T_{PB} as defined by Biggs, 1996) is indeed about half as long (60 days) as for the second peak (120 days). We suppose that summer temperatures might favour bacterial activity, although winter temperatures could moderate such activity. A close association between temperature and microbial growth in biofilms has also been demonstrated in drinking water distribution systems (Lund & Ormerod, 1995; Ndiongue, Huck & Slawson, 2005). Moreover, previous studies in marine waters have mentioned a stronger temperature dependence of microbial respiration as compared with photosynthesis (Pomeroy & Deibel, 1986; Hancke & Glud, 2004). In our model, a temperature limitation term for bacterial activity generated a temperature-dependant loss. As a consequence (Fig. 4), such a loss might have controlled the biomass dynamics in the first peak while in the second peak no self-generated loss was likely to occur. In low temperature conditions only hydrodynamics would have controlled biomass loss, as modelled by Uehlinger *et al.* (1996).

Our study confirmed that dynamics of the epilithic biomass is mainly driven by hydrodynamics, which plays a substantial role in biomass loss through a discharge-dependant detachment. Regarding the biological processes, our study outlined that epilithic biomass resulted from a phototrophic growth, which was quite insensitive to temperature and a heterotrophic bacteria mediated loss, which was strongly dependant on temperature. In disturbed streams or in low temperature conditions, the hypothesis that epilithic biomass results from the equilibrium between a phototrophic growth and a discharge dependant detachment is reliable as the bacteria-mediated heterotrophic loss is negligible while hydrodynamics control prevails. Conversely during extended periods of flow stability and favourable temperature, i.e. in typical summer low water period, the self-generated detachment because of heterotrophic processes should be considered to accurately model epilithic biomass.

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