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Modelling periphyton dynamics in running water

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Abstract

The short-term biomass dynamics of periphyton communities in running water is characterized by deep variations. This temporal variability is mainly produced by changes in running water velocity. The shear force caused by the friction of water over the surface of the periphyton produces a removal of biomass and creates open sites for colonization. Running water also brings new suspended algae that can establish on open sites. An increase in the velocity of the water can also improve the renewal of nutrients in depleted areas and the elimination of waste products, producing higher reproductive rates. In this paper, we have developed a model of periphyton biomass dynamics taking the water velocity and nutrient concentration as external driving variables influencing immigration, removal and reproductive rate of the algae. We fitted the model to field data encompassing high and low water velocities and different seasons. We have qualitatively compared the parameters obtained from different situations with the expected ones based on bibliographic information. The model has shown a good fit to field data and parameters were similar to expected ones, giving evidence that the model provides a good description for the processes that dominate the periphyton dynamics in running waters. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The community of microscopic algae that grow attached to a variety of submerged substrata is an essential component of lotic ecosystems. This community, called periphyton, is responsible for most of the primary production (McIntire, 1973; Apesteguia and Marta, 1979), and constitute the food source for several invertebrates and fishes (Cattaneo et al., 1993). It also plays a major role in the metabolic conversion and partial removal of biodegradable material in rivers and streams (Lau and Liu, 1993).

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Water velocity and nutrient concentrations are among the most important factors influencing periphyton biomass in streams (Stevenson, 1983; Reiter, 1986). These factors can fluctuate stochastically, induced by rainfall, human activity, etc. This could generate the high spatial and temporal variability of periphyton biomass observed in field studies (Morin and Cattaneo, 1992). Seasonal oscillations are largely driven by changes in the abiotic environment during the year, but the short-term dynamics can be more influenced by hydraulic disturbances produced by spates (McCormick and Stevenson, 1991).

The bulk of water that is directly over the surface of periphyton is called boundary layer (BL). In this layer, flows are modified by friction between water and substrate, reducing horizontal velocity and creating the boundary layer flow velocity gradient (BFG). Water velocity increases with distance from the substrate along an axis perpendicular to the substrate surface. Flow is turbulent throughout most of the BL, but there is a laminar sublayer (LS) immediately adjacent to the substrate. The thickness of the LS is inversely proportional to current velocity, while turbulence is directly proportional to current velocity (Stevenson, 1983).

Three important processes occur in the BL that influence periphyton dynamics:

- Nutrient uptake: the increase of current velocity enhances algal growth by reducing the thickness of the relatively nutrient depleted LS. This produces a steeper BFG, increasing the rate of molecular diffusion across the BL (Whitford, 1960; McIntire, 1968; Horner et al., 1990).
- Particle attachment: any organism that could fix to the substrate must be transported through the LS. Attachment rate increases with current velocity because the thickness of LS decreases (Stevenson, 1983).
- Particle removal: the shear stress brought about by water, increases with current velocity, enhancing the removal of periphyton cells. Other factors, such as roughness, and the periphyton development, can modify this shear stress (Reiter, 1986).

There are a few quantitative models of the biomass of periphyton dynamics (Horner et al., 1983; Stevenson, 1986; Biggs, 1988; Momo, 1995). Only one of these (Momo, 1995) tries to explain the temporal variability of the biomass and none of these account for the discrete and stochastic nature of disturbance events produced by high discharge episodes. The models of Horner et al. (1983) and Momo (1995) include current velocity as a variable in continuous time equations (differential equations), but the model of Stevenson (1983) does not include it at all.

We built a mechanistic model of biomass dynamics, trying to describe the high variability found in field data. The model was based on the interaction between colonization, detachment and growth, and has current velocity and nutrient concentration as external variables. The model was formalized by means of a discrete difference equations, fitted to field data, and qualitatively compared with other published data.

2. Model formulation

The temporal dynamics of the periphyton biomass is represented by a discrete iterative equation:

$$B_{t+1} = I_t + C_t - D_t \tag{1}$$

where B_{t+1} (mg chl-a m^{-2}) is the biomass at time $t+1$, I_t is the growth function, C_t is the colonization function and D_t is the detachment function at time t. All of these functions are expressed in mg chl-a m^{-2} and described in detail below.

Although it is well known that grazing could affect periphyton structure and species composition, it is often assumed that grazing on periphyton growing, over artificial substrata, is negligible (Stevenson, 1986).

The results of Cattaneo et al. (1993) suggest that the division of the community into functional units is the most efficient basis for modelling. We have modeled total biomass to use the simplest mathematical representation and the simplest way to obtain field data to compare with the model.

2.1. Growth

We assume that density-dependent decreases in light availability and nutrient supply may occur in the periphyton. When the community develops into thicker mats, light penetration and nutrient diffusion decrease (Riber and Wetzel, 1987; Stevenson et al., 1991).

We follow the approach of Getz (1991, 1993): the growth model is based upon a resource uptake function G and a conversion of extracted resource function F:

$$I_t = B_t \cdot F(G) \tag{2}$$

where B_t is the biomass at time t.

Getz (1991) assumes a $F(G)$ that is increasing and concave in G on the assumption that the more consumption of a particular resource, the more potential the population has to grow.

$$F(G) = \rho \cdot (1\text{-}1/G) \tag{3}$$

where $\rho > 0$ is an upper bound to the growth rate per unit of biomass.

We use a modified Holling type II response function with respect to the nutrient concentration near the surface of the periphyton R_t (mg l^{-1}).

$$G(R_t, B_t) = \frac{\delta . R_t}{\beta + R_t + \gamma \cdot B_t} \tag{4}$$

where $\delta > 0$ is the maximum extraction rate, $\beta \geq 0$ (mg l^{-1}) is the half-saturation parameter and γ (mg m^2 mg-chl-a^{-1} l^{-1}) is a self-interference parameter (Szathmary, 1991).

We introduce the effect of current velocity, V_t (cm s^{-1}), assuming R_t as a linear function of V_t and nutrient concentrations Nc_t (mg l^{-1}) at time t (Riber and Wetzel, 1987; Horner et al., 1990).

$$R_t = \mathrm{Nc} \cdot (r_1 + r_2 \cdot V_t) \tag{5}$$

where r_1 and r_2 (s cm^{-1}) are the coefficients of the linear function.Then the final equation for the growth sub-model is:

$$I_t = B_t \cdot \rho \cdot \left(1 - \frac{\beta + R_t + \gamma \cdot B_t}{\delta \cdot R_t}\right) \tag{6}$$

If the function R_t is constant, the Eq. (6) can be reduced to a logistic, applying an appropriate substitution of parameters (Getz, 1993).

2.2. Colonization

The current velocity can influence both immigration and emigration from the water to the matrix of the periphyton. The immigration rate depends on current velocity because the laminar sublayer becomes thinner as the velocity rises and the algae must be transported through it to reach the substrate (Stevenson, 1983). Thus, current velocity has a positive effect on immigration rates. This effect is counteracted by a stronger shear stress over the periphyton produced by a higher current velocity. Moreover, the alteration of the substrate environment produced by the maturation of the attached community can be an important force modifying the immigration and emigration rates (Stevenson, 1983). One of the simplest ways to simulate this behavior is a parabola:

$$C_{\mathrm{t}} = c_1 \cdot V_t^2 + c_2 \cdot V_t B_t + c_3 \tag{7}$$

where $c_1 \leq 0$ (mg chl-a s^2 m^{-4}), $c_2 \geq 0$ (s m^{-1}) and $c_3 \geq 0$ (mg chl-a m^{-2}) are constant coefficients.

At high current velocity, the colonization can be negative. This simulates a net emigration, which refers to the removal of individual cells or small groups of cells from the surface of periphyton.

2.3. Detachment

Sloughing is the detachment of relatively large particles of biomass whose characteristic size is comparable to, or greater than, the thickness of the periphyton layer (Stewart, 1993). These are the typical events produced by the spates. The disturbance produced by these high discharge events may be the major mechanism controlling biomass in streams (Biggs and Thomsen, 1995).

The development of the periphyton community may result in the growth of several layers of cells. When the algae in the inner layer die due to a lack of light and/or nutrients, the probability of detachment of this patch of algae increases. Thus, an increase in the biomass of periphyton raises the detachment probability. Moreover, a greater biomass loss occurs when the current velocity is higher than the mean velocity under which the algae have been developed (Horner et al., 1990). This relationship between velocity and sloughing can be represented by a quadratic term, which takes into account the effect of shear stress over the surface of the periphyton (Silvester and Sleigh, 1985; Gordon et al., 1992). Therefore, we derived the following expression:

$$D_t = d_1 \cdot B_t \cdot (V_t - V_\mathrm{m})^2 \tag{8}$$

where V_m (m s^{-1}) is the mean current velocity during the development of the periphyton, V_t (m s^{-1}) the actual current velocity, B_t the biomass and $d_1 \geq 0$ (s^2 m^{-2}) is the degree of sloughing produced when current velocity is higher than the mean velocity. When V_t is lower than V_m the function value is zero. We use current velocity as a forcing variable because it is easy to measure in the field and is considered the most appropriate descriptor of the disturbance regime (Biggs, 1995).

3. Model fitting

We used biomass time series collected for other purposes in a third-order plain stream, a tributary of the Luján River in Argentina (see Giorgi and Malacalza, 1994 for details about the study site). The time series have a span of 45 days. Biomass was estimated as mg chl-a m^{-2} following the modified Lorenzen method (Aminot, 1983). A wooden platform containing 16 cm^2 ceramic plates was fixed to the bottom of the stream. For biomass estimation, three plates were taken every ≈ 3 days. The current velocity (cm s^{-1}) was measured at the same time.

Two sampling locations were used; station two (upstream site) and station three (downstream site); station one was not used for the model calibration because the time series were incomplete. In each station two sites were picked out, one with current velocity lower than 15 cm s^{-1} (2L, 3L) and one with velocities higher than 15 cm s^{-1} (2R, 3R). The time series were collected in two seasons (winter and summer).

Time series length was ≈ 11 points, so we could not fit all the ten parameters accurately. We use the information from Figs. 7 and 9 of Horner et al. (1990) to adjust the parameters of the R_t function (Appendix A), and the field data for the remaining parameters.

The values of soluble reactive phosphorus concentration (Nc_t) were fixed at 1 mg SRP l^{-1}, which is the mean concentration values for this stream (Feijoó et al., 1996). We assumed that the Nc_t variation in the sampling period was not very important for the biomass dynamics of the periphyton.

For the fitting and simulation of the model, we fixed the time step at 12 h, obtaining the values of the current velocity at each time step by linear interpolation.

To fit the model parameters to the field data we have chosen an observation error, which in most cases produced accurate and precise point estimates (Pascual and Kareiva, 1996). We used a weighted least squares loss function based on a lognormal distribution to minimize the observation error:

$$\sum \frac{[\log(B_t) - \log(\hat{B}_t)]^2}{\mathrm{LVar}_t} \tag{9}$$

where B_t is the biomass value from field data, $\hat{B}_t$ the estimated value and LVar_t the variance of the log transformed biomass replications for the time t.

In the first stages of the minimization process, we used an adaptive simulated annealing algorithm (Ingber, 1989, 1993) to find the global minimum. After that, the generalized reduced gradient nonlinear optimization code (Microsoft Corporation, 1994) was used to fine-tune the parameter values.

4. Model simulations

Stochastic simulations varying the values of velocity and nutrients were performed in order to contrast the model response against already published results. For each level of each external environmental variable (nutrients or velocity), we performed 200 runs of the model using the fitted parameters. In each run, the model was simulated for 200 time steps, and the last 50 biomass values were used to calculate the average for this particu-

Table 1
Fitted parameters for all sites and seasons, mean velocity (V_m) and loss function values

	2L		2R		3L		3R	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
ρ	1.66	1.32	1.28	1.31	2.44	3.69	1.14	1.06
δ	7280.63	223.16	17.21	447.31	28.07	10.92	15.63	773.40
β	17619.45	0.045	0.0033	16242	43.57	102.71	0.28	517.67
γ	0	11.80	2.50	0	0	0.15	0.0041	10.66
c_1	0	0	−0.00066	0	0	−0.041	0	−0.00026
c_2	0	0	0	0.017	0	0	0	0
C_3	32.20	0.10	3.34	0.030	8.38	16.68	0.34	1.43
D_1	0.02	0.010	0.0027	0.0044	0	0.028	0.0055	0.00047
V_m	7	16	54	56	0	18	54	64
Loss	27.73	4.95	15.86	4.35	99.66	52.61	43.24	5.27

lar simulation. The velocity and nutrient time series for the simulations were generated as follows:

$$Z_t = \bar{Z} + \varepsilon \tag{10}$$

where Z_t is the external variable (nutrients or velocity) at time t, $\bar{Z}$ the mean value and a normal random variable with mean zero and variance σ^2.

The response to velocity was obtained from simulations with different mean velocities. These values where chosen from a close to zero up to twice the mean field velocity for each case, keeping the standard deviation and the nutrient concentration values constant. The response of the model to nutrient concentration was determined using values from 0.1 to 5 mg l^{-1}, keeping the coefficient of variation as 0.5 and using the field velocity values. Because values of Z_t lower than 0 were not possible, the normal distribution was truncated at 0 in the cases where it was necessary.

We performed a deterministic stability analysis of the model using the leading eingenvalue λ of the jacobean (May et al., 1975). Although the model is stochastic, the deterministic stability analysis was able to predict the effect of parameters on simulated dynamics (Taylor, 1992).

Because our model is one-dimensional, the only eigenvalue is λ. The eigenvalue measures the rate of increase of a small perturbation around the equilibrium value. More specifically, disturbances grow exponentially if $1 < \lambda$, damp exponentially if $0 < \lambda < 1$, damp with oscillations if $-1 < \lambda < 0$, and grow in oscillatory way if $\lambda < -1$.

We analyzed the effect of concentration and velocity on the stability, computing λ with different values of the external variables.

5. Results

The model had a good fit to the time series (Fig. 1). The influence of the current velocity through the autogenous growth, colonization and detachment submodels were enough to describe the fluctuations observed in the field data. The worst case was the winter-3L time series, where the model clearly did not describe the fluctuations observed. The current velocity for this time series was zero during the entire sampling interval, thus others factors not included in the model probably produced the biomass fluctuation. The loss function Eq. (9) for the winter-3L time series had the highest value (Table 1), and the second highest value was ≈ 50% of this, so there was a clear differentiation between the fit of this time series and the remainder. The time series corresponding to high current velocity sites had lower loss function value than the low current velocity sites (Table 1) showing a better fit to the field data (Fig. 1).

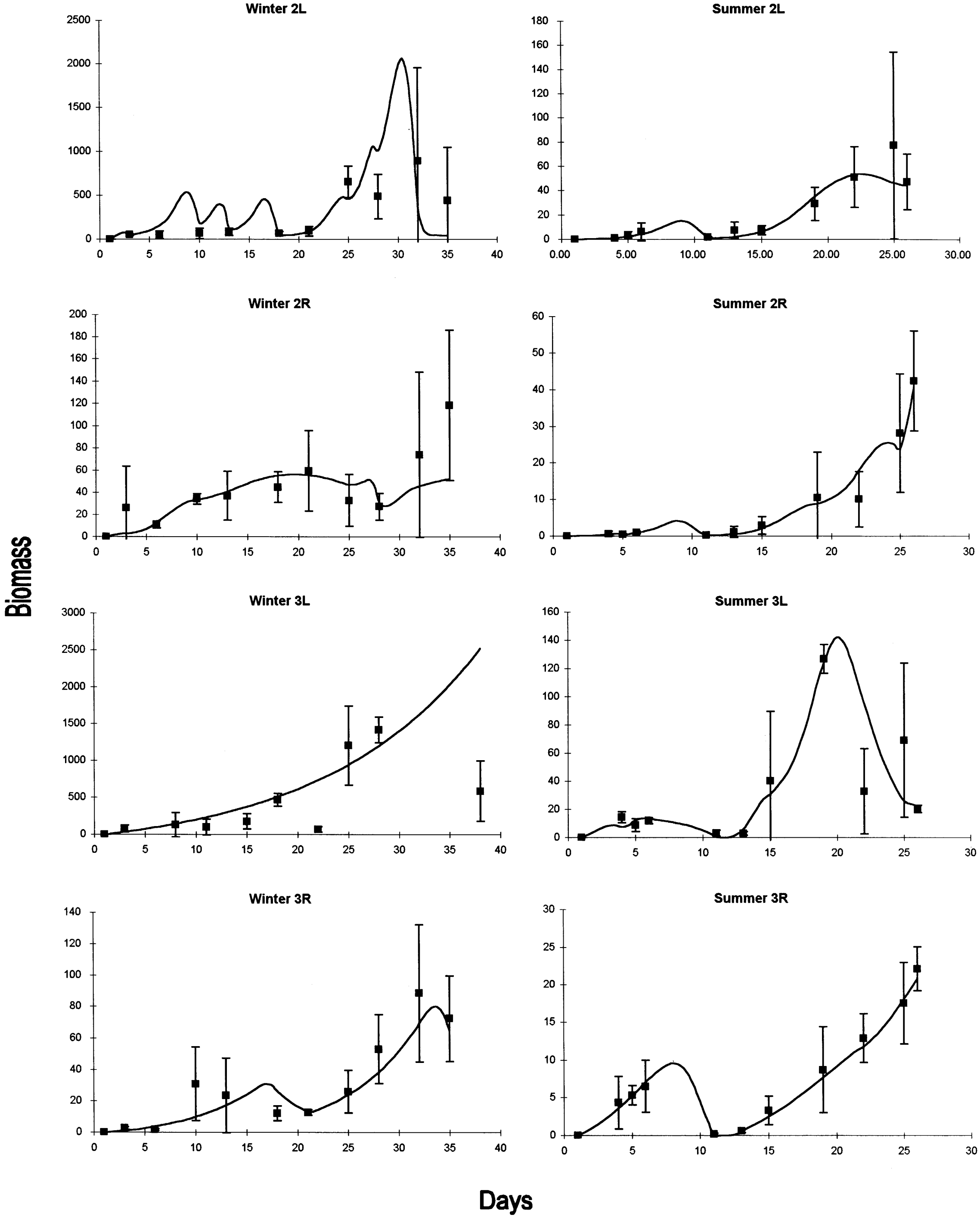

Fig. 1. Field biomass vs time. Squares represent field biomass mean values (mg chl-a m^{-2}) and bars are standard deviations. Bold curves are the model fitted outputs.

The maximum growth rate ρ was similar between seasons for each site, suggesting that the community is responding to some site-attributes that do not change throughout the year.

The maximum extraction rate δ, showed higher values in winter for the low velocity sites, but in summer for the high velocity ones. The lack of seasonality of ρ is in some way compensated by the clear pattern of variation of δ across the seasons.

The half saturation parameter β showed very high values in 60% of the cases. This means that, for those cases, the saturation in the nutrient uptake will be reached at unrealistic high nutrient concentrations. However only in the winter-3R case we observed that the saturation was reached at a reasonable nutrient concentration. The summer-2L and winter-2R cases had higher γ values, shifting the saturation zone to higher nutrient concentrations.

The self-interference parameter γ is related to density-dependent processes associated with the nutrient uptake. This parameter was zero in 36% of the cases and in general higher in summer than in winter. This pattern coincides with the reduction of light incidence produced by the developing of floating hydrophytes, such as *Lemna gibba* (Giorgi and Malacalza, 1994).

The overall pattern for the colonization submodel was that 50% of the cases showed a constant immigration rate ($c_1 = 0$ and $c_2 = 0$). The parameter c_1 determines the strength migration of individual cells and was different from zero in three cases showing very low values. This implies that individual migration was not important compared with sloughing. Only the summer-3L case showed an enhanced immigration rate with the increase in biomass, where the parameter c_2 was greater than zero.

The degree of sloughing produced when current velocity was higher than the mean, was greater in low velocity sites, meaning that the changes in current velocity had a greater influence at these sites than in the rapid current ones.

The different cases had almost the same qualitative response to changes in mean current velocity. They always showed an optimum current velocity where the highest biomass was observed (Fig. 2). The responses at velocities higher than the optimum, generally fell more abruptly than at lower velocities. The peak of biomass usually was reached at values near the mean velocity experienced by the community (Fig. 2, Table 1). The response of the model for the winter-3L time-series was an artifact because the current velocity was zero and the parameters related to velocity were not fitted.

We found three qualitative biomass responses to the nutrient concentration (Fig. 3): a linear increase (summer-2L, winter-2R, summer-3L), an exponential increase (winter-2L, summer-2R, winter-3L) and a response showing a maximum (winter-3R, summer-3R). The third response was the one observed in field studies (Giorgi, 1995) but the maximum biomass values were observed at lower concentrations of nutrients in the field.

The deterministic stability analysis showed that the model was stable only for thin strips with the parameter fitted for winter-2L, summer-2R, winter-3L, summer-3L and winter-3R time-series (Fig. 4). The winter-2R and summer-3R showed a more extended region of stability and the summer-2L was stable in almost all the range of nutrients and current velocity.

The nutrient concentration had almost no influence on stability in the summer-2L, winter-3R and winter-3R. Instead, it had a major influence at low velocities for the summer-2R, winter-2L, winter-3L, summer-3L and summer-3R time-series. These results showed a broad range of possible responses of the system to changes in current velocity and nutrients.

6. Discussion

The maximum growth rate (ρ) remained almost constant for each site. So, the current velocity has a very limited influence on this parameter and each site maintained some characteristics across seasons and sites. This pattern could be related to geomorphology-controlled patterns (Mulholland et al., 1995).

The parameters related to nutrient uptake, maximum extraction rate (δ), half saturation (β) and self-interference (γ) show a broad range of

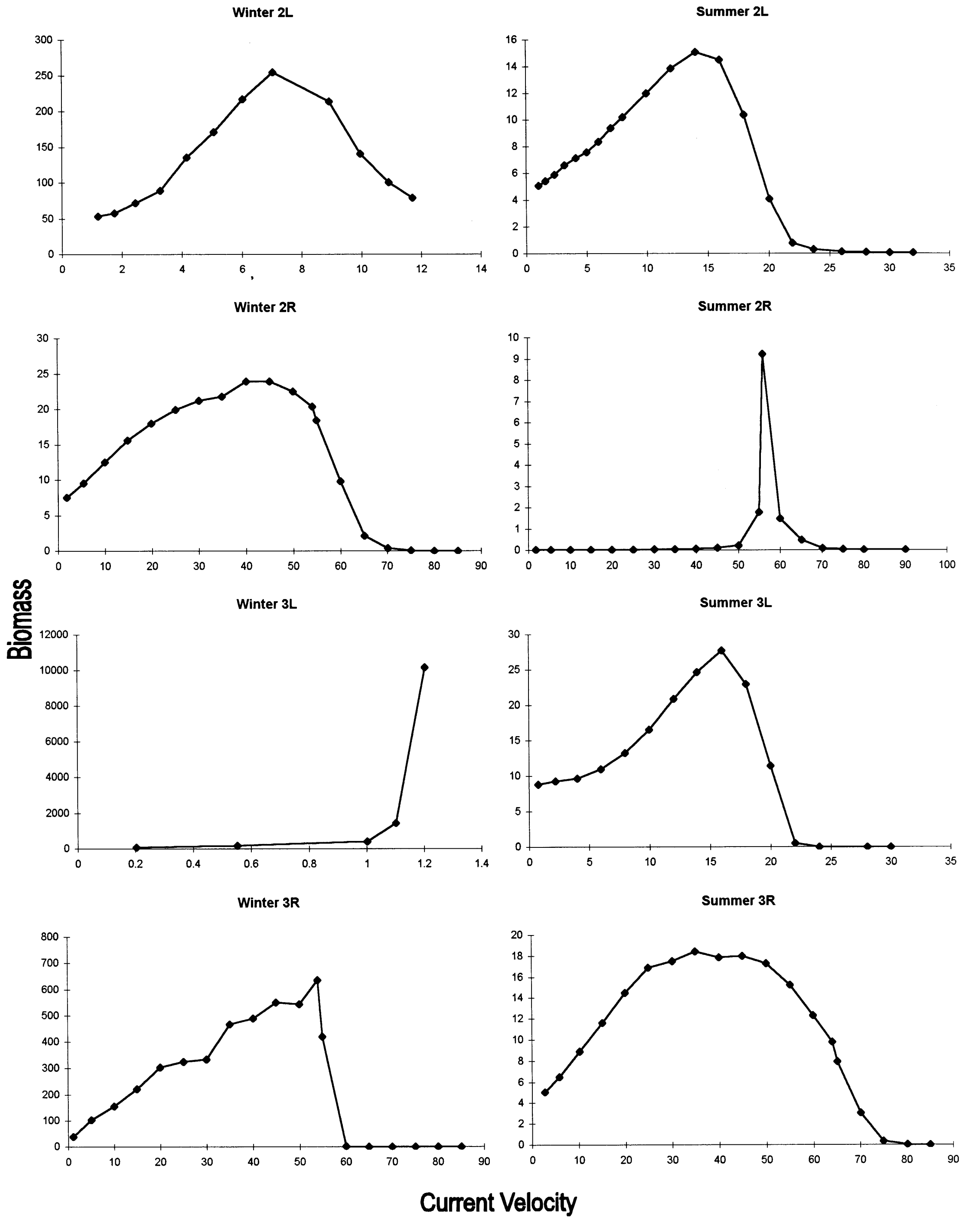

Fig. 2. Biomass response to current velocity (cm s^{-1}). Each point is the result of averaging biomass values (mg chl-a m^{-2}) of 200 stochastic simulations.

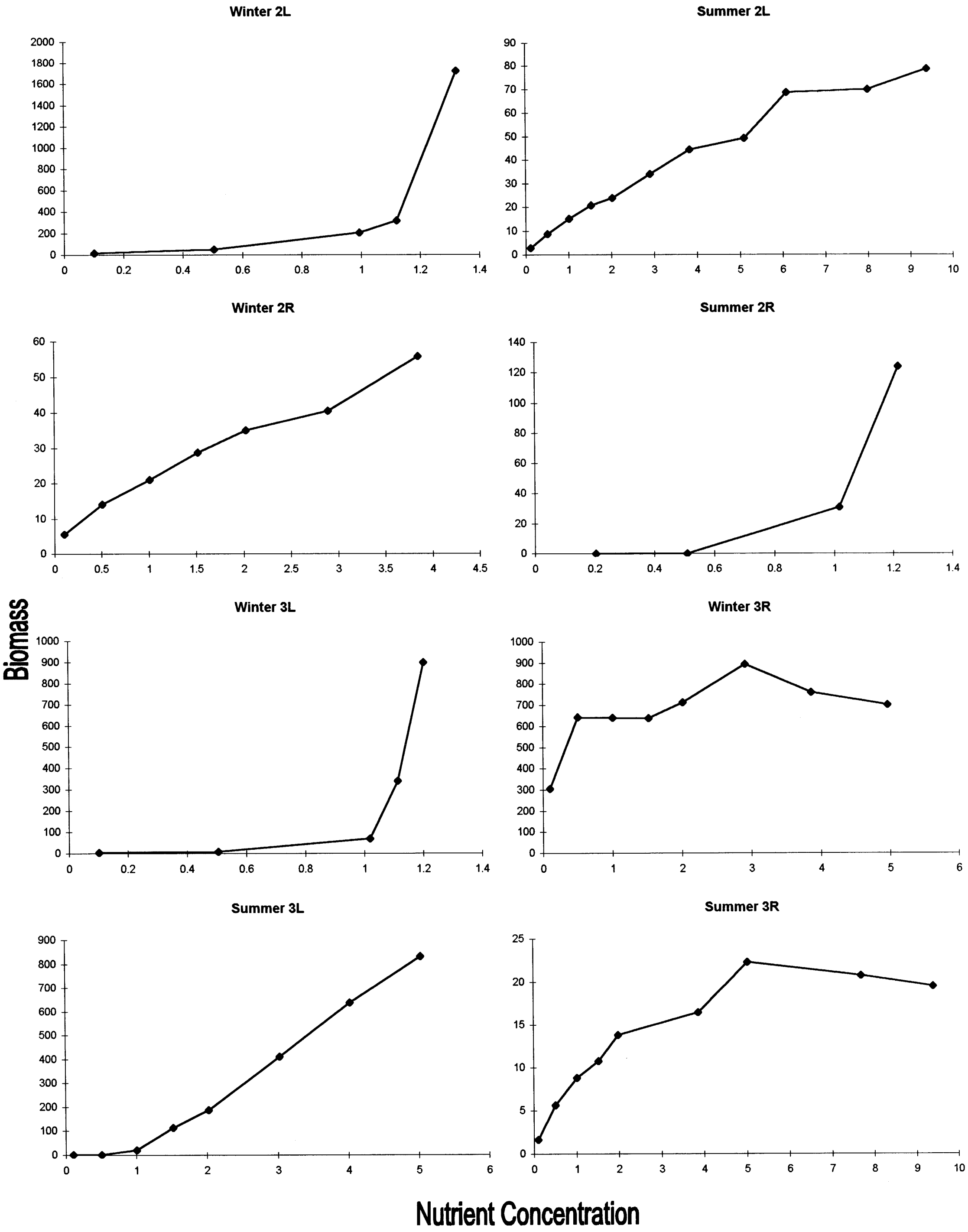

Fig. 3. Biomass response to nutrient concentration (mg SRP l^{-1}). Each point is the result of averaging biomass values (mg chl-a m^{-2}) of 200 stochastic simulations.

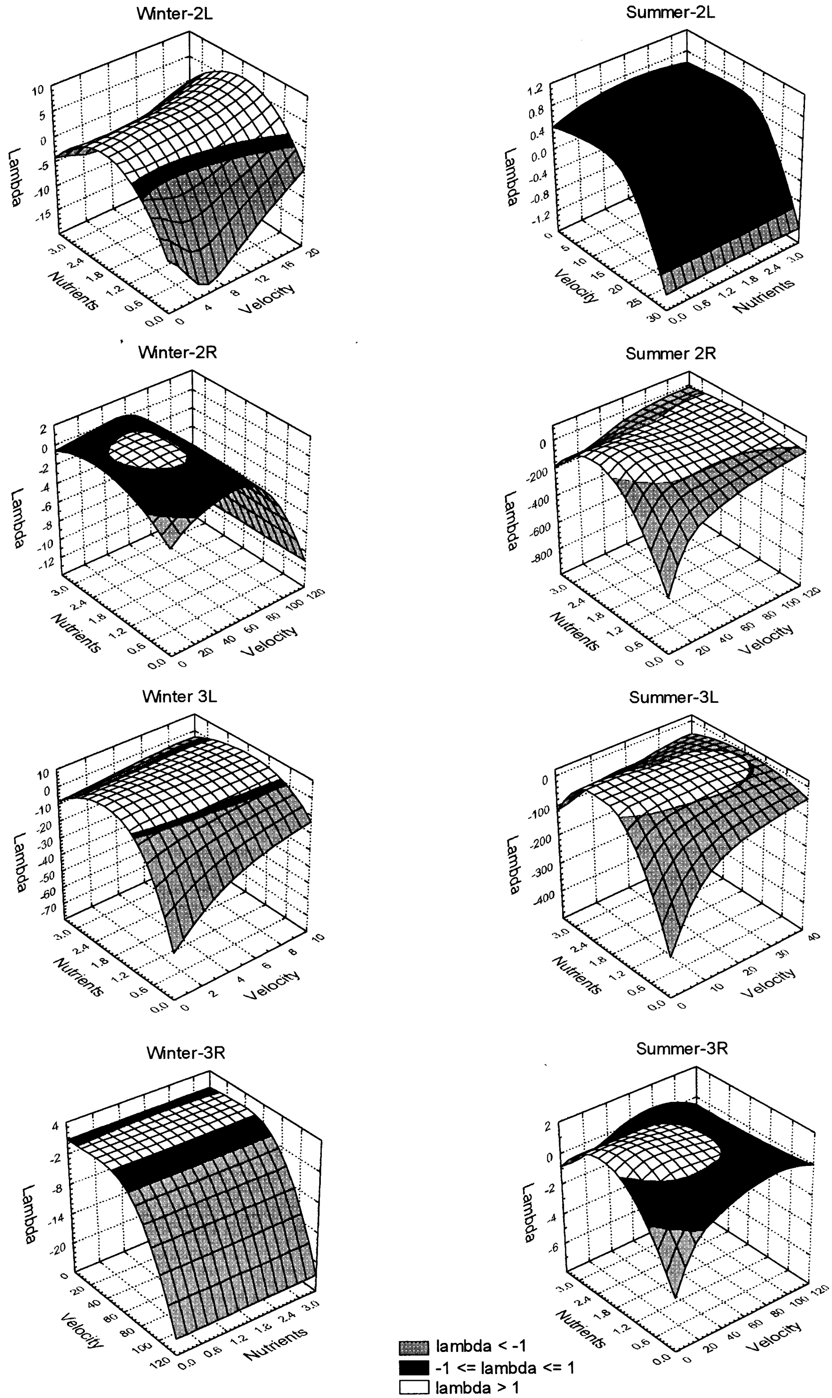

Fig. 4. Stability vs nutrients (mg SRP l^{-1}) and velocity (cm s^{-1}). The values of the Eigenvalue, λ (lambda), > -1 and < 1 corresponds to the stability zone.

values, but the resulting pattern of uptake is roughly the same: a linear increase of uptake with the increase of nutrient concentration, without showing saturation in the range of nutrient concentrations used in the simulations (up to 10 mg SRP l^{-1}). The experimental evidence for communities of a stream of the same basin showed that biomass reaches a maximum value at 1.5 mg SRP l^{-1} (Giorgi, 1995). This is not in agreement with our results, and may be a consequence of the lack of a detailed nutrient concentration record.

Comparing the different sites, current velocity considerably affects the constant settlement rate (c_3). Low current velocity sites have higher values of c_3 than high current velocity sites. These last results are in complete concordance with experimental evidence (Biggs and Stokseth, 1996).

We modeled explicitly the dependence of immigration on current velocity through the parameters c_1 and c_2, but the influence of velocity was shown mostly through c_3. Thus, the immigration pattern is influenced by the velocity but at a seasonal time scale.

The values of d_1 indicate that variations in velocity would affect the sites with low current more than sites with high velocity. This pattern was found by Horner and Welch (1981) and probably is caused by the low shear force pressure suffered by the algae in the low current sites. The algae are weakly attached to the substrate so a small rise of the current velocity results in a higher loss of biomass.

The response of biomass to changes in current velocity was similar to that observed in previous studies realized in field and laboratory (Horner and Welch, 1981; Horner et al., 1990, Humphrey and Stevenson, 1992). This response consisted of two phases. First, there is an increase of mean biomass with increase in current velocity. This phase is characterized by the predominance of the positive effects of current velocity: an enhancement of nutrient uptake. When biomass reached a maximum, the second phase starts and the negative effects of current velocity begin to predominate.

When we related mean biomass with mean nutrient concentration we found two patterns. The main one is an exponential increase in biomass with the increase in nutrient concentrations. This is not a realistic pattern in the simulated range of concentrations. The second pattern is qualitatively similar to the predominant one for velocity, showing a peak biomass at some nutrient value; the concentration values at which this peak is produced are very high. These responses are a consequence of the values of the uptake function parameters.

The model has a great variety of dynamic behaviours that could describe the different situations observed in field and laboratory studies. In an early study, the immigration rate was found to increase with biomass (Stevenson, 1983) but in a second field study no relationship between biomass and immigration was found (McCormick and Stevenson, 1991). Both behaviours can be simulated with our model although we found a predominance of the last one.

The analysis of stability shows a variety of responses to external variables (Fig. 4). In general, the model became more unstable when current velocity and nutrient concentrations were either very low or very high. Thus, the biomass of environments with these characteristics should have a greater variability than other habitats. This variability pattern has not been previously studied in periphyton communities (however, see Cattaneo et al., 1993). Therefore, streams with high or low levels of both current velocity and nutrient concentrations will be more unpredictable and difficult to manage.

For the short-term, the good fit of the model shows that current velocity and autogenic factors are the most important factors controlling biomass dynamics. This behaviour is in agreement with field evidence from the same stream (Giorgi and Malacalza, 1994). Biggs and Close (1989) discussed that current velocity and nutrients concentrations are both necessary for the characterization of the periphyton dynamics. We included in the model the nutrient concentration and use a constant value taken from field data (Feijoó et al., 1996). However, no nutrients field data was measured at the time the biomass and velocity were sampled. Therefore, we would expect that a more detailed measurement of this environmental variable and its inclusion on the fitting process could produce a better result.

This model could be expanded to describe the seasonal biomass dynamics with the inclusion of additional environmental variables, such as light intensity and temperature.

The model also gives a plausible quantification of the biological mechanisms operating in periphyton communities, pointing out the importance of the interaction between autogenic growth and physical (hydrodynamic) control. The model allows us to predict the observed complex dynamics under some combination of parameters and, particularly shows that periphyton is a very unstable system whose dynamic is highly influenced by the stochastic fluctuations of the environment.

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Appendix A

The paper of Horner et al. (1990) analyzed the responses of periphyton to changes in current velocity and phosphorous concentration. With the information from two figures, the areal uptake of soluble reactive phosphorous (SRP) in relation to biomass (Fig. 7) and the areal uptake rate of SRP in relation to velocity (Fig. 9), we could fit the function G:

$$G(R_t, B_t) = \frac{\delta.Nc_t.(r_1 + r_2.V_t)}{\beta + Nc_t.(r_1 + r_2.V_t) + \gamma.B_t}$$

where Nc_t is the in channel SRP concentration (μg 1^{-1}), B_t the biomass (mg chl-a m^{-2}) and V_t the channel velocity. The calculated uptake rate G were then used to fit the observed uptake rate. The values of the fitted parameters were: $\delta = 1.15$; $\gamma = 0.0017$; $\beta = 0$; $r_1 = 2.86$ and $r_2 = 0.81$.

References

Aminot, A., 1983. Dosage de la chloropyhlle et des phéopigment par spectrofhotometric. In: Aminot, A., Chausspied, M. (Eds.) Manuel des analyses chimiques en Milieu Marin, Centre National pour L'Eplotation des Océans, Quebec, p. 184.

Apesteguia, C., Marta, J., 1979. Producción de biofilm en ambientes acuáticos del río Paraná Medio. II: Medición de la velocidad de producción media e instantánea. Rev. Asoc. Cienc. Nat. Litoral. 10, 39–48.

Biggs, B.J.F., 1988. Algal proliferation in New Zeland's shallow, stony foothills-fed rivers: towards a predictive model. Verh. Internat. Vereing. Limnol. 23, 1405–1411.

Biggs, B.J.F., 1995. The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. Freshwat. Biol. 33, 419–438.

Biggs, B.J.F., Close, M.E., 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. Freshwat. Biol. 22, 209–231.

Biggs, B.J.F., Thomsen, H.A., 1995. Disturbance of stream periphyton by perturbations in shear stress: time to structural failure and differences in community resistence. J. Phycol. 31, 233–241.

Biggs, B.J.F., Stokseth, S., 1996. Hydraulic habitat suitability for periphyton in rivers. Reg. Riv. Res. Manag. 12, 251–261.

Cattaneo, A., Legendre, P., Niyonsenga, T., 1993. Exploring periphyton unpredictability. J. N. Am. Benth. Soc. 12, 418–430.

Feijoó, C.S., Momo, F.R., Bonetto, C.A., Tur, N.M., 1996. Factors influencing biomass and nutrient content of the submersed macrophyte *Egeria densa* Planch. in a pampasic stream. Hydrobiologia 341, 21–26.

Getz, W.M., 1991. A unified approach to multispecies modeling. Nat. Res. Model. 5, 393–421.

Getz, W.M., 1993. The logistic equation revisited: final instalment. Tree 8, 68–71.

Giorgi, A., 1995. Response of periphyton biomass to high phosphorus concentration in laboratory experiments. Bull. Environ. Contam. Toxicol. 55, 825–832.

Giorgi, A., Malacalza, L., 1994. Biomass variation of microphytobenthos in plain stream. Verh. Internat. Verein. Limnol. 25, 1883–1887.

Gordon, N.D., McMahon, T.A., Finalyson, B.L., 1992. Stream Hydrology: An Introduction for Ecologists. Wiley, Brisbane, p. 526.

Horner, R.R., Welch, E.B., 1981. Stream periphyton development in relation to current velocity and nutrients. Can. J. Fish Aquat. Sci. 38, 449–457.

Horner, R.R., Welch, E.B.,Veenstra, R.B. 1983. Development of nuisance periphytic algae in laboratory streams in relation to enrichment and velocity. In: Wetzel, R.G. (Ed.) Periphyton of Freshwater Ecosystems. Dr W. Junk Publishers, The Hague, pp. 121–134.

Horner, R.R., Welch, E.B., Seeley, M.R., Jacoby, J.M., 1990. Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. Fresh. Biol. 24, 215–232.

Humphrey, K.P., Stevenson, R.J., 1992. Responses of benthic algae to pulses in current and nutrients during simulation of subscouring spates. J. N. Am. Benthol. Soc. 11, 37–48.

Ingber, L., 1989. Very fast simulated reannealing. Math. Comput. Model. 12, 967–973.

Ingber, L., 1993. Simulated annealing: practice versus theory. J. Math. Comput. Model. 18, 29–57.

Lau, Y.L., Liu, D., 1993. Effect of flow rate on biofilm accumulation in open channels. Wat. Res. 27, 335–360.

May, R.M., Conway, G.R., Hassell, M.P., Southwood, T.R.E., 1975. Time delays, density-dependence and single species oscillations. J. Anim. Ecol. 43, 747–770.

McCormick, P.V., Stevenson, R.J., 1991. Mechanisms of benthic algal succession in lotic environments. Ecology 72, 1835–1848.

McIntire, C.D., 1968. Physiological ecological studies on benthic algae in laboratory streams. J. Water Pollut. Control Fed. 40, 1940–1952.

McIntire, C.D., 1973. Periphyton dynamics in laboratory streams: a simulation model and its implications. Ecol. Mon. 43, 399–420.

Microsoft Corporation. 1994. Microsoft Excel 4.0 User's Guide 2, p. 353.

Momo, F.R., 1995. A new model for periphyton growth in running waters. Hydrobiologia 299, 215–218.

Morin, A., Cattaneo, A., 1992. Factors affecting sampling variability of freshwater periphyton and the power of periphyton studies. Can. J. Fish Aquat. Sci. 49, 1695–1703.

Mulholland, P.J., Marzolf, E.R., Hendricks, S.P., Wilkerson, R.V., Baybayan, A.K., 1995. Longitudinal patterns of nutrient cycling and periphyton characteristics in streams: a test of upstream-downstream linkage. J. N. Am. Benthol. Soc. 14, 357–370.

Pascual, M.A., Kareiva, P., 1996. Predicting the outcome of competition using experimental data: maximun likelihood and bayesian approaches. Ecology 77, 337–349.

Reiter, M.A., 1986. Interactions between the hydrodynamics of flowing water and the development of a benthic algal community. J. Fresh. Ecol. 3, 511–517.

Riber, H.H., Wetzel, R.G., 1987. Boundary layer and internal diffusion effects on phosphorus fluxes in lake periphyton. Limnol. Oceanogr. 32, 1181–1194.

Silvester, N.R., Sleigh, M.A., 1985. The forces on microorganisms at surfaces in flowing water. Fresh. Biol. 15, 433–448.

Stevenson, R.J., 1983. Effects of currents and conditions simulating autogenically changing microhabitats on benthic diatom immigration. Ecology 64, 1514–1524.

Stevenson, R.J., 1986. Mathematical modeling of epilithic diatom accumulation. In: Ricard, M. (Ed.), Proceedings of the Eighth Diatom Symposium. Koeltz Scientific Books, Koenigstein, pp. 323–335.

Stevenson, R.J., Christopher, P.G., Kirschtel, D.B., King, C.C., Tuchman, N.C., 1991. Density dependent growth, ecological strategies, and effects of nutrients and shading on benthic diatom succession in streams. J. Phycol. 27, 59–69.

Stewart, P.S., 1993. A model of biofilm detachment. Biotech. Bioeng. 41, 111–117.

Szathmary, E., 1991. Simple growth laws and selection consequences. Trend. Ecol. Evol. 6, 366–370.

Taylor, A.D., 1992. Deterministic stability analysis can predict the dynamics of some stochastic population models. J. Anim. Ecol. 61, 241–248.

Whitford, L.A., 1960. The current effect and growth of freshwater algae. Trans. Am. Micro. Soc. 79, 302–309.