



Predicting the biomass of periphyton and macroinvertebrate functional feeding groups in stream reaches

Journal:	<i>River Research and Applications</i>
Manuscript ID:	draft
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Schweizer, Steffen; Eawag Switzerland, Siam Reichert, Peter; Eawag, Siam
Keywords:	Benthos, Periphyton, Invertebrates, Functional Feeding Groups, Modelling, prediction uncertainty, river ecology, river rehabilitation



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Predicting the biomass of periphyton and macroinvertebrate functional feeding groups in stream reaches

S. Schweizer¹, M. E. Borsuk¹, U. Uehlinger¹, S. Bouletrêau²
and P. Reichert^{1*}

¹ *Eawag: Swiss Federal Institute of Aquatic Science and Technology,
8600 Dübendorf, and ETH Zürich, Switzerland*

**Corresponding author, e-mail peter.reichert@eawag.ch*

² *Laboratoire d'Écologie des Hydrosystèmes,
UMR 5177 CNRS-Université Paul Sabatier, Toulouse, France.*

1
2
3 **Abstract:** Periphyton and invertebrates are important components of the trophic cascade in
4 running waters due to their ability to produce organic material, decompose detritus, and serve
5 as a food source for organisms at higher trophic levels. River rehabilitation (e.g. local habitat
6 improvement or reach-scale widening of the river bed) often changes the morphological and
7 hydraulic conditions of the river, affecting the development of periphyton and invertebrates.
8 However, few predictive models exist which can support decision-making (e.g. where and
9 how to conduct a rehabilitation activity). To provide such predictions, an integrative model is
10 necessary that represents the cause-effect relations between rehabilitation alternatives and
11 morphological, hydraulic, and ecological consequences. This paper describes simple
12 statistical periphyton and invertebrate models that can serve as submodels of such an
13 integrative model. For model development and calibration, we used data on periphyton from
14 8 sites (3 different rivers, total sample size 286) and invertebrates from 2 sites (1 river,
15 sample size 86) to derive a predictive river benthos model. Linear and non-linear regression
16 analyses revealed that periphyton is most strongly influenced by the time since the last bed-
17 moving flood and hydraulic conditions (in particular, flow velocity), whereas invertebrate
18 functional groups are predominantly dependent on seasonality. For total invertebrates,
19 collector-gatherers, and predators, regression models could be developed with R^2 values
20 between 0.52 and 0.71. The representation of scrapers was somewhat less satisfying.
21 Shredders and filterers were significantly less abundant in our data set and were therefore not
22 modelled. Model development and complexity were severely limited by the small number of
23 complete data sets available. Additional long time series data on periphyton and invertebrate
24 density from different rivers together with values of important variables influencing the
25 benthos community dynamics, would be extremely useful to improve such simple prediction
26 models.
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2 **Keywords:** Benthos, periphyton, invertebrates, functional feeding groups, modelling, non-
3
4 linear regression analysis, river ecology, scrapers, collector-gatherers, predators, river
5
6 rehabilitation, prediction uncertainty.
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Peer Review

1. INTRODUCTION

Careful planning of river rehabilitation requires predictions of the expected response of the river morphology and ecosystem to proposed management actions. To produce such predictions, we are developing an integrative river rehabilitation model (IRRM) (Reichert et al. 2007, Schweizer et al. 2007b, Spörri et al. 2007, Borsuk et al. 2006) which represents important cause-effect relations between critical influence factors and river system attributes. Together with a model of the stakeholders' preference structure for different levels of these attributes (Hostmann et al. 2005), the IRRM is intended to provide a comprehensive basis for supporting river rehabilitation decisions (Reichert et al. 2007). The present paper describes the benthos community submodel for the IRRM.

Periphyton and invertebrates are primary and secondary producers in running waters that dominate the first levels of the trophic pyramid in many small and intermediate size rivers. While algae use radiation and nutrients to produce organic material, invertebrates perform diverse ecological functions and feed on various food bases: scrapers on periphyton; collector-filterers and -gatherers on organic material in the running water and sediment, respectively; shredders primarily on allochthonous inputs of leaves, seeds and small branches from the shoreline vegetation; and predators on other invertebrates. The next higher level of the trophic cascade is composed of fish which feed on macroinvertebrates and some additionally on periphyton (Power et al 1989). In this vein, periphyton and invertebrates exhibit bottom-up control on the complete ecological system of running waters. Furthermore, periphyton and invertebrates (mainly through their effect on periphyton) have a strong influence on oxygen and nutrient concentrations, pH, and the content of organic material, due to their metabolism (Reichert et al. 2001). From the socio-economic perspective, periphyton and macroinvertebrates exert further important influences on the river and its users. Blooms of algae or macrophytes reduce the cross-sectional area of a river and its flow velocity resulting in higher water levels (Bretschneider & Schulz 1985) and increasing the probability

1
2 and frequency of dike overtopping. Moreover, algal blooms negatively affect the aesthetic
3 value of a river and thus decrease the river's recreation potential. Since invertebrates gather
4 or filter organic material from the river bed and flowing water, they influence water colour,
5 clarity and odour. Moreover, anglers rely on fish abundance which depends partly on the
6 availability of macroinvertebrate biomass. These relations indicate that successfully
7 predicting the benthos community in a river is essential for understanding the river ecosystem
8 and its response to rehabilitation efforts.
9
10
11
12
13
14
15
16
17
18

19 Several previous attempts have been undertaken to model the dynamics of periphyton
20 and macroinvertebrate biomass in river reaches. These attempts can be divided into
21 mechanistic population dynamic models and statistical approaches that empirically relate
22 abundance of functional groups to important external influence factors. Mechanistic models
23 generally give better and more detailed insights into the ongoing processes within a system.
24 However, as these models represent a relatively large number of processes, they tend to be
25 overparameterized, making it difficult to estimate model parameters from empirical data
26 alone. The large data requirement of such models also makes it difficult to have
27 measurements from a sufficient number of sites for a cross-system fitting procedure (e.g.
28 Borsuk et al. 2001). This makes most applications of such models site-specific and leads to a
29 lack of universality that would be required for prediction. Statistical approaches describe less
30 detail of ecosystem function, which reduces their data requirements. For this reason, it is
31 easier to develop a more universal model calibrated using data from several study sites
32 jointly. The smaller data requirements also make it easier to use such models predictively.
33 On the other hand, prediction accuracy is limited by the simpler modelling approach.
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54

55 One of the pioneers in mechanistic modelling of lotic ecosystems is McIntire (1973)
56 who developed a periphyton model and a hierarchical model for biomass of periphyton and
57 invertebrate functional feeding groups (grazers, shredders, collectors and predators). Power
58 et al (1995) modelled the food-web dynamics in large rivers linking physical and biological
59
60

1
2 processes. They aggregated species of a hypothetical river food web into four functional
3
4 groups (detritus, vegetation, grazers, predators) intended to represent the dominant resources
5
6 and consumers in a river food chain. Unfortunately, no comparison between model
7
8 simulations and measured data are given in these publications. Uehlinger et al. (1996)
9
10 presented mechanistic periphyton models for the Necker River (Switzerland) describing
11
12 periphyton growth, detachment, and loss due to floods. These models considered the effects
13
14 of temperature, light, discharge, periphyton density limitations on growth and detachment
15
16 rates. Their best model shows a good agreement with measured data. However, the
17
18 derivation of the model is based on a data set from only one site at the Necker River.
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
Boulêtreau et al (2006) adapted this model to two sites of the Garonne River (France) and
introduced an additional term to account for temperature-dependent, self-generated loss due
to heterotrophic processes in the biofilm. We have used the datasets of both Uehlinger et al
(1996) and Bouletreau et al (2006) in the derivation of the periphyton models presented in
this paper.

Lamouroux et al. (2004) analyzed the relationships between habitat (characterized by
hydraulic conditions (Froude Number), substrate size and benthic particulate organic matter)
and the functional structure of invertebrate communities at three spatial scales (microhabitat,
stream reach, basin) with a statistical model. They found good correlations for deposit
feeders (collector-gatherers who feed on coarse organic matter in the river bed), and fair
associations for shredders and scrapers. Yoshimura et al (2006) focused on the prediction of
functional ratios of the different feeding groups of macroinvertebrates to relate them to
ecosystem attributes. These ratios were found to depend on dissolved oxygen and organic
carbon, periphyton cover and organic halogen compounds. Other approaches have used
artificial neural networks as a “black box” model structure for describing the dependence of
invertebrate abundance on external influence factors (e.g. Gevrey et al 2003, Park et al 2003)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42

In this article, we develop a statistical model for predicting periphyton and invertebrate biomass in rivers as a function of the major influence factors. In contrast to “black box” statistical approaches, after preliminary linear regression analyses, we develop a nonlinear model formulation that represents the expected response as a mechanistically derived function of the influence factors. This attempts to combine the advantages of a statistical model formulation (minor data requirements, joint evaluation of several data sets) with a simple parameterization of what we expect to be the behaviour of a mechanistic model. We expect that this will lead to more robust behaviour of the model, particularly when extrapolating outside its calibrated range of influence factors. In addition to these statistical approaches, a mechanistic model simulating periphyton and invertebrate functional groups in one of the rivers investigated in this study (the Sihl River) is being developed and reported separately (Schuwirth et al., 2007). This will provide improved understanding of the benthos community dynamics in this river, but will require many more data from other rivers to achieve universal model parameter values. We hope that the parallel development along these two research lines will lead to improved insight into benthic community dynamics and that the relationships discovered with the statistical approach will support the process of improving mechanistic models.

43
44
45
46
47
48
49
50
51
52

The remainder of this paper is structured as follows: We begin by describing the study sites and data sources. We then describe our modeling procedures. Next, we present and discuss the results and, finally, draw our conclusions.

53 54 55

2. STUDY SITES AND DATA

56
57
58
59
60

The data used to derive the periphyton models presented in this article were collected by previous studies at the Swiss rivers, Necker (4 sites) and Sihl (2 sites), and the French river, Garonne (2 sites). Since no accompanying invertebrate studies at the sites of the Necker and

1
2 Garonne were conducted, only invertebrate data from the Sihl River could be used to derive
3
4 the invertebrate models.
5
6

7 8 **Sihl** 9

10 The Sihl River is a prealpine Swiss river flowing into the Limmat River in the city of Zürich.
11 Its catchment is predominated by pasture and forest. Since the construction of the Sihl
12 reservoir (Sihlsee) in 1937 for hydropower generation, the flow regime of the Sihl River has
13 been reduced artificially to a constant discharge between 2.5 - 4.0 m³/s, promoting river bed
14 siltation and algal proliferation due to the absence of bed disturbances (Elber et al 1996).
15
16 Between 1990 and 1992, several artificial floods were released from the Sihlsee to investigate
17 the morphological and ecological responses to attempts at mimicking a more natural flow
18 regime.
19
20
21
22
23
24
25
26
27
28
29

30 In two campaigns (May 1990 - August 1990 and April 1991 - July 1992) (Elber et al
31 1992, Elber et al 1996), total periphyton biomass as well as invertebrate abundance and total
32 biomass were measured irregularly every 1-4 weeks at two locations at the Sihl River. The
33 first site (“upstream”) is located in a typical flowing reach while the second (“downstream”)
34 is situated in the backwater zone of a weir (at 1.5 km distance from the upstream site), with a
35 lower mean velocity and grain size and a modestly higher water depth (Table 1). Figure 1,
36 panel A, shows maximum daily discharge and standing biomass (in g ash free dry biomass
37 (AFDM) / m²) over the study period at both sites.
38
39
40
41
42
43
44
45
46
47
48

49 Invertebrates were sampled with a surber sampler (30cm x 30cm) at six locations over
50 the complete wetted river width. Invertebrates were identified to family or genus level and,
51 where reasonable, to species level. In Figure 1, panel B, the pattern of total invertebrates (in
52 dry weight / m²) over time is depicted.
53
54
55
56
57
58

59 Further details on the methods of data collection are described by Elber et al (1992) and
60 Elber et al (1996).

1
2
3
4 For the Sihl River, further processing of data was necessary to transform abundance
5 data of invertebrates to biomass estimates for the functional feeding groups. The mean
6 specific body mass (mass per individual) of the most important species or higher taxonomic
7 groups was evaluated from the literature. Total biomass was then calculated as the measured
8 abundances multiplied by the corresponding mean specific body masses. Finally, the biomass
9 estimates of the different taxa were aggregated according to their functional feeding groups
10 (see Schuwirth et al. 2007 for more details).
11
12
13
14
15
16
17
18
19
20
21
22
23
24

25 **Necker**

26
27 The Necker, a prealpine, 6th order river in the eastern part of Switzerland has its sources at an
28 elevation of about 1300 m a.s.l.. About 30% of its catchment area is forested, the remainder
29 is pasture land. Agricultural runoff and inflow of treated sewage have increased the
30 concentrations of inorganic phosphorus and nitrogenous compounds above reported limiting
31 concentrations for the growth of benthic algae (Table 1). The flow regime is rather
32 unpredictable, since bed-moving spates may occur at any time of the year (Fig. 1, panels C
33 and D).
34
35
36
37
38
39
40
41
42
43
44

45 **Necker Downstream**

46
47 From October 1992 to the beginning of March 1994, periphyton was monitored at two
48 riffles/runs and two pools at the site “Necker Downstream” (Uehlinger et al 1996). Samples
49 were taken every two weeks (Fig. 1, panel C) and periphyton biomass was determined as
50 AFDM / m². A more detailed description of the study site and sampling methods are given by
51 Uehlinger et al. (1996).
52
53
54
55
56
57
58
59
60

Necker Aachsäge

Nine sites were sampled at the Necker Aachsäge site (Uehlinger 1991): five in the main channel and four on a partially inundated bar and one in a side channel, which was formed during the investigation. From the end of February 1989 until March 1990 all sites were sampled biweekly (Fig. 1, panel D). Periphyton biomass for each morphological type (main channel, inundated bar, side channel) was determined as AFDM/m². Uehlinger (1991) gives a more detailed description of the methods and study sites.

Garonne

The Garonne River is a large river located in southwest France with pebble banks and a mean daily discharge of 150 m³/s at Toulouse, an urban centre with approximately one million inhabitants (Boulêtreau et al 2006). Study sites were located 36 km upstream (site Aouach, 6th order) and 12 km downstream (site Gagnac, 7th order) of Toulouse (Table 1). During the low water period (from July to October), the mean discharge is reduced to about 50 m³/s and the river is characterized by a shallow (<1.5m) and wide profile (100m).

Sampling was conducted from July 2001 to December 2001 at weekly intervals and then monthly until November 2002 (Fig. 1, panel E). For each study site, a reference point was chosen in a riffle. At this reference point, sampling was performed at each date at three distinct depths of the cross section: 30, 50 and 70 cm. Biomass values (in AFDM / m²) of the three depths were then averaged to provide biomass measurements for each date at each site. The recorded biomass is not representative of the biomass occurring at all points of the cross section but satisfactorily describes the low depth region where epilithic biofilm typically develops (Améziane et al 2002). A more detailed description of the study sites and sampling methods is given by Boulêtreau et al (2006).

3. MODELING METHODS

The goal of our modelling effort was to obtain parsimonious statistical models that consider the most important factors influencing the biomass of the functional groups. Such models cannot describe all relevant processes in detail, but they should also not be a “black-box” model formulation, unrelated to known system behaviour. To derive such models, we used a four-step approach: (i) the important influence factors for the functional groups were identified based on the analysis of scatterplots and systematic linear regressions of combinations of influence factors and their transformations, (ii) a nonlinear model was formulated that considers the most important influence factors identified with the linear model but that can be expected to have a more robust behaviour when applied to different rivers and for extrapolations beyond the range of influence factors, (iii) the sensitivity of model fits to the values of parameters that could not be fitted was performed, and (iv) a model selection procedure was carried out by jointly fitting a series of submodels of this nonlinear model to the data of as many sites as possible. For the selected model, an uncertainty analysis with respect to model results was performed.

Table 2 summarizes the variables considered as potential predictive influence factors in the river benthos model.

3.1 Preliminary Analysis of the Significance of Influence Factors

In the linear regression approach, all linear models based on one, two or three influence factors or their square root, inverse, log or square transformations were systematically considered to find the model that provides the best fit to the data. This led to a ranking of the most important factors influencing the biomass of each functional group.

3.2 Formulation of Nonlinear Model

As described in the Results section, time since the last bed-moving flood was found to be the most significant influence factor, particularly for periphyton. Therefore, the nonlinear model must provide a reasonable phenomenological description of the development of periphyton after bed movement. As the linear models indicate, a proportional increase in periphyton biomass with time after the flood already provides a good description of observations. However, due to the increasing instability of a benthic biofilm with increasing thickness, this cannot be an adequate description for long times after the flood. For this reason, we seek a model formulation that describes linear growth of biomass with time immediately after a flood, but reaches saturation over time. If k_B is the slope of the initial increase, B_{\max} is the biomass saturation value, Δt_{flood} is the time after the last bed-moving flood, and B denotes current biomass, then

$$B = \frac{B_{\max} \cdot k_B \cdot \Delta t_{\text{flood}}}{B_{\max} + k_B \cdot \Delta t_{\text{flood}}}$$

is such a process formulation. We generalized this approach by adding limiting effects with increasing water depth and flow velocity and decreasing gravel size, by allowing for nonlinearity of the increase as a function of the time since the last bed-moving flood, and by adding a seasonal dependence. This led to the following model formulation:

$$B = \frac{\overline{B_{\max}} \cdot \overline{k_B} \cdot \Delta t_{\text{flood}}^b}{\overline{B_{\max}} + \overline{k_B} \cdot \Delta t_{\text{flood}}^b} l(h, v, d_{50}, \Delta t_{\text{jul}}) \quad (1)$$

where

$$l(h, v, d_{50}, \Delta t_{\text{jul}}) = \exp(-\gamma h) \cdot \exp(-\delta v) \cdot \frac{d_{50}}{k_{d_{50}} + d_{50}} \max \left(1 + \alpha \cos \left(2\pi \cdot \frac{\Delta t_{\text{jul}} - \Delta t_{\text{jul}}^{\max}}{1y} \right), 0 \right) \quad (2)$$

describes the limiting effect of mean water depth, h (m), mean flow velocity v (ms^{-1}), and median gravel grain size, d_{50} (m), as well as seasonal variation (through the time within the

year, Δt_{jul} (Julian days)). The model parameters in equations (1) and (2) have the following interpretations: $\overline{k_B}$ is the maximum (with respect to h , v , and d_{50}) and mean (with respect to seasonality) coefficient describing benthic biomass growth after a flood ($\text{g/m}^2/\text{d}^b$), $\overline{B_{\text{max}}}$ is the maximum (with respect to h , v , and d_{50}) and mean (with respect to seasonality) asymptotic biomass after long times after the last flood occurred (g/m^2), b is the exponent of Δt_{flood} (-), $\Delta t_{\text{jul}}^{\text{max}}$ is the time within the year (Julian Days) at which standing crop would be maximum for constant values of the other influence factors, k_{d50} is the grain size with half saturation for $\overline{k_B}$ and $\overline{B_{\text{max}}}$ (m), α is the relative amplitude of the seasonal variation (relative to the mean) (-), and γ (m^{-1}) and δ (m^{-1}s) are the parameters describing limitation by water depth and flow velocity (1y = 1 year).

For short times after the last flood, this model behaves as:

$$B \approx \overline{k_B} \cdot \Delta t_{\text{flood}}^b \cdot l(h, v, d_{50}, \Delta t_{\text{jul}}) \quad \text{for } \Delta t_{\text{flood}} \ll \left(\overline{B_{\text{max}}} / \overline{k_B} \right)^{1/b} \quad (3a)$$

Long after the last flood, this model asymptotically approaches a biomass that depends only on the limiting factors h , v , and d_{50} , and on the season (through Δt_{jul}):

$$B \approx \overline{B_{\text{max}}} \cdot l(h, v, d_{50}, \Delta t_{\text{jul}}) \quad \text{for } \Delta t_{\text{flood}} \gg \left(\overline{B_{\text{max}}} / \overline{k_B} \right)^{1/b} \quad (3b)$$

This general model was used to describe the behaviour of all functional groups in the river, despite the smaller importance of time since the last flood for invertebrates compared to periphyton.

3.3 Parameter Estimation

The model given by the equations (1) and (2) has a more realistic asymptotic behaviour than the linear models. On the other hand, because of the larger number of parameters it can be expected to have worse identifiability. The most obvious example of the trade-off between a realistic formulation of asymptotic behaviour and identifiability is the dependence of biomass

on time since the last flood. Increase after the flood is characterized by the parameter $\overline{k_B}$, asymptotic biomass by $\overline{B_{\max}}$. If a data set does not contain measurements of biomass for long times after a flood, $\overline{B_{\max}}$ is not identifiable. Nevertheless, a model that includes this saturation effect is more realistic when applied to times long after a flood if we use a realistic estimate for $\overline{B_{\max}}$ from the literature.

To account for model structure uncertainty and measurement error, the deterministic model was extended by a random error term. Because of the heteroscedasticity of the error in original biomass density units (larger error for larger values of functional group biomass density), the error was assumed to be additive to Box-Cox transformed model results (Box and Cox, 1964, 1982) rather than to the predicted biomasses directly. This transformation of biomass, B , is given by the following equation

$$g(B) = \begin{cases} \frac{(B + \lambda_2)^{\lambda_1} - 1}{\lambda_1} & \lambda_1 \neq 0 \\ \ln(B + \lambda_2) & \lambda_1 = 0 \end{cases} \quad (4)$$

where λ_1 (-) and λ_2 (g/m^2) are parameters that can be adjusted to improve the fit of the empirical distribution of the residuals to that generated by the model. As a function of the model parameters, $\boldsymbol{\theta} = (\overline{k_B}, \overline{B_{\max}}, b, \gamma, \delta, k_{d50}, \alpha, \Delta t_{\text{jul}}^{\max})$, external influence factors, $\mathbf{x} = (\Delta t_{\text{flood}}, h, v, d_{50}, \Delta t_{\text{jul}})$, and the error term, E (g/m^2) ^{λ_1} , the probabilistic predictions of biomass B^{prob} (g/m^2) are then given by

$$B^{\text{prob}}(\boldsymbol{\theta}, \mathbf{x}) = g^{-1}(g(B(\boldsymbol{\theta}, \mathbf{x})) + E) \quad (5)$$

where $B^{\text{prob}}(\boldsymbol{\theta}, \mathbf{x})$ is the deterministic function given by equations (1) and (2). With appropriate adjustments of the parameters λ_1 and λ_2 of the Box-Cox transformation, the residuals of transformed model results and data could be shown to approximately follow a normal distribution with constant variance. Therefore, maximum likelihood parameter

1
2 estimation could be performed by applying the unweighted least-squares regression function
3
4 “nls” of the statistics and graphics package R (<http://www.r-project.org>).
5
6

7 8 **3.4 Sensitivity Analysis** 9

10 Due to identifiability problems, some parameters had to be kept at a fixed value that could not
11 be estimated from the data. Other parameters were then estimated for different values of such
12 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
13 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
14 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
15 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
16 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
17 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
18 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
19 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed
20 parameters to evaluate the sensitivity of the parameter estimates on the values of fixed

21 22 **3.5 Model Structure Selection** 23

24 Setting α , γ or δ equal to zero, or b equal to unity, leads to simplified submodels that do not
25 consider seasonality of the dynamics, dependence on mean water depth and flow velocity, or
26 nonlinearity in recovery after a flood, respectively. By analyzing the loss in the quality of fit
27 when setting one of these parameters to zero (α , γ or δ) or unity (b), we obtained an
28 assessment of the importance of the corresponding influence factor in describing the data.
29 Together with an assessment of the estimated parameter values, this trade-off between
30 simplicity and quality of fit was used to select the final model for each functional group.
31
32
33
34
35
36
37
38
39
40

41 42 **3.6 Uncertainty Analysis** 43

44 Prediction uncertainty of the finally selected models was estimated by propagating the
45 uncertainty in the estimated parameters as well as a 20% uncertainty in the parameters not
46 included in the statistical fit, and adding the error term accounting for model structure and
47 measurement error. A multivariate normal distribution was used to describe parameter
48 uncertainty. This distribution was truncated to avoid negative values of the parameters for
49 which negative values do not have a reasonable interpretation ($\overline{k_B}$, $\overline{B_{\max}}$, b , k_{d50}). Monte
50 Carlo simulation was used to get a sample from the distribution of model results. As the
51 probabilistic model predictions, B^{prob} , are given by equation (5), this required a five step
52
53
54
55
56
57
58
59
60

1
2 procedure: (i) a random sample was drawn from the multivariate parameter distribution, (ii)
3 this sample was propagated through the model to the results, (iii) these results were
4 transformed using the Box-Cox transformation, (iv) the normally distributed error term was
5 added, and (v) the results were transformed back to original units by applying the inverse
6 Box-Cox transformation.
7
8
9
10
11
12
13
14
15
16
17
18
19

20 4. RESULTS

21
22
23 In this section, we present the results of the modelling approach discussed in the previous
24 section as applied to the data sets of periphyton from the Sihl, Necker and Garonne rivers and
25 to the data sets of total invertebrates and their dominant functional groups (scrapers,
26 collector-gatherers, and predators) from the Sihl river. While the model is not explicitly
27 dynamic, the daily model predictions can be calculated from daily data of the influence
28 factors. This is a convenient way of representing model results and comparing them with
29 measured data. Still it has to be kept in mind that the linear and nonlinear regression
30 relationships are calculated based on average depth, velocity and grain size, and that only
31 time since the last flood and seasonality (in Julian Days) provide the dynamics of the
32 predictions.
33
34
35
36
37
38
39
40
41
42
43
44
45
46

47 The shape of the empirical distribution of the residuals was critically analyzed after
48 performing the fits. Without applying the Box-Cox transformation (see equations 4 and 5)
49 there was strong heteroscedasticity of the residuals with a much larger variance for large
50 values of the observations than for small ones. We obtained best results when setting $\lambda_1 = 0.3$
51 for all modelled functional groups and $\lambda_2 = 1$ gAFDM/m² for periphyton, $\lambda_2 = 1$ gDM/m² for
52 total invertebrates, and $\lambda_2 = 0.1$ gDM/m² for the functional groups of invertebrates. (Because
53 it represents a sort of “offset parameter”, it is expected that the value of λ_2 will vary according
54
55
56
57
58
59
60

1
2 to the range of values of each measured variable). These values led to the elimination of
3
4 heteroscedasticity for periphyton and collector-gatherers, and to a significant reduction in
5
6 heteroscedasticity for scrapers and predators. Also, normal quantile-quantile plots showed
7
8 significantly less deviation from normality.
9

10
11 Table 3 shows the results of the fits performed for sensitivity analysis and model
12
13 structure selection for all functional groups. For each functional group, parameter estimates
14
15 are shown for a base model (model x.1), for models with modified values of the parameters
16
17 that were not estimated (models x.2 and x.3; to analyze the sensitivity of parameter estimates
18
19 and fit quality to the selected values), and for simplified models that omit one or several
20
21 influence factors (models x.4 to x.9; for model structure selection). In addition to the
22
23 parameter estimates, for each fit, the number of fitted parameters, n , and the correlation
24
25 coefficient between measurement and predictions, R^2 , are given. This comparison of fit
26
27 results allows us to make an assessment for the degree in quality of fit we lose by omitting an
28
29 influence factor from the analysis. To avoid identifiability problems, best estimates of the
30
31 saturation biomass, $\overline{B_{\max}}$, and the half-saturation gravel diameter, k_{d50} , were specified in all
32
33 base models. The lack of data after long periods without floods and the small spread in
34
35 gravel size across the sites did not allow us to estimate these parameters. Nevertheless, we
36
37 decided to include these influence factors to make the model more robust when applied
38
39 outside its calibration range. The value of k_{d50} was selected according to Biggs & Price
40
41 (1987), the saturation biomass, $\overline{B_{\max}}$, was chosen based on survey data of Austrian rivers
42
43 (Yoshimura et al 2006). As many fewer data were available for invertebrates, a simpler base
44
45 model had to be chosen. This was done by setting the parameter of the velocity dependence
46
47 term, δ , to zero for all invertebrate data analyses (preliminary fits with inclusion of this
48
49 parameter led to unsatisfying parameter estimates). In Table 3, the model finally selected
50
51 (see below for rationale), is indicated by a bold model identifier in the second column. The
52
53
54
55
56
57
58
59
60

parameter estimates, including standard deviations and correlation coefficients, for these models are given in the appendix.

Periphyton

The linear regression analyses revealed that the influence factor “time since last bed-moving flood” (Δt_{flood}) was by far the most significant predictor for estimating periphyton biomass, followed by water temperature and photosynthetically active radiation (PAR) over the last 14 days. Apparently, the concentrations of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) were sufficiently high to avoid nutrient limitation of periphyton growth.

The structure of the periphyton model (equations 1 and 2) directly formulates the dependence on the time since the last flood. The influence of radiation and temperature on periphyton growth and standing crop are included indirectly by the term describing the seasonal effects.

The Swiss rivers (Necker, Sihl) differ from the French river (Garonne) with respect to size (mean discharge, depth) (Table 1) and frequency of disturbance (Fig. 1). Thus, the data from the more stable (in terms of frequency of disturbance) Garonne River provide some information on the saturation biomass, $\overline{B_{\text{max}}}$, while the data from the more flood prone Swiss rivers are better able to provide information on the coefficient describing the increase of biomass after a flood, $\overline{k_B}$. Nevertheless, the estimates of $\overline{B_{\text{max}}}$ for different choices of the model structure varied over so wide ranges, that we cannot rely on these estimates. Data from only one river that also differs considerably from the other rivers in the values of other influence factors seem not to be sufficient to provide a reliable estimate of this parameter.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

The models 1.2 and 1.3 (when compared to model 1.1) in Table 3 show that even drastic changes of the values of the fixed parameters $\overline{B_{\max}}$ and k_{d50} did not strongly affect the quality of the fit (compare the values of R^2 between these models). With the exception of the parameters $\Delta t_{\text{jul}}^{\max}$ and α , the values of the estimated parameters do not change very strongly when the fixed parameters are changed. This is an indication that $\Delta t_{\text{jul}}^{\max}$ and α are poorly identifiable. This is confirmed by the very small values of α for all fits which indicate a minor seasonal component and thus provide the cause for the poor identifiability.

The models 1.4 to 1.7 in Table 3 demonstrate the effect of omitting the seasonal dependence ($\alpha = 0$, making $\Delta t_{\text{jul}}^{\max}$ irrelevant), the effect of water depth ($\gamma = 0$), the effect of flow velocity ($\delta = 0$), and the nonlinearity of increase after a flood ($b = 1$). The results (R^2) clearly show that omission of seasonality (model 1.4), omission of depth dependence (model 1.5) and omission of nonlinearity of increase after a flood (model 1.7) only leads to a minor decrease in the quality of the fit. On the other hand, consideration of velocity dependence seems to be important (model 1.6 leads to a considerable drop in R^2). Model 1.8 demonstrates that even the combined omission of the three less relevant influence factors does not lead to a significant drop in R^2 . Adding depth dependence in model 1.9 did not improve the fit significantly. For this reason, model 1.8 with only two fitted parameters is obviously the best compromise between model complexity and quality of fit.

Figure 2 illustrates the behaviour of model 1.8 as compared to measured data from all sites.

Invertebrates

Exploratory linear regression models for total invertebrate, collector-gatherer, and predator biomass performed fairly well, with R^2 values exceeding 0.6. However, the results of linear

1
2 regression models for scraper biomass were significantly worse ($R^2 = 0.38$). Linear
3
4 regression results for shredder and collector-filterer biomass were even worse ($R^2 = 0.19$ and
5
6 0.32 respectively). Due to the low biomass of these last two functional groups (< 6 % of total
7
8 biomass), they were not included in the further model development.
9
10

11 As mentioned before, due to the lack of data from several rivers, we had to choose a
12
13 simplified base model for invertebrates. From the model used for periphyton (equations 1
14
15 and 2) we omitted the velocity dependence term by setting $\delta = 0$ because including this term
16
17 did not lead to reasonable parameter estimates. Starting from this base model, we performed
18
19 a similar sensitivity analysis and model selection procedure as for periphyton (see Table 3).
20
21 The values of $\overline{B_{\max}}$ and k_{d50} were again chosen according to typical values found in
22
23 Yoshimura et al (2006) and Biggs & Price (1987).
24
25
26
27
28
29

30 As expected for parameters that are poorly identifiable because of their low influence on
31
32 model results (in contrast to parameters that are poorly identifiable because of strong
33
34 correlations), a change in the values of $\overline{B_{\max}}$ and k_{d50} had only a small effect on parameter
35
36 estimates and a very small effect on the performance of the fit (compare the R^2 values of the
37
38 models x.2 and x.3 with x.1 for $x = 2, 3, 4$ and 5 in Table 3).
39
40
41
42

43 The models x.4 to x.6 in Table 3 ($x = 2, 3, 4$ and 5) demonstrate the effect of omitting
44
45 the seasonal dependence ($\alpha = 0$, making $\Delta t_{\text{jul}}^{\max}$ irrelevant), the effect of water depth ($\gamma = 0$),
46
47 and the nonlinearity of increase after a flood ($b = 1$). The results (R^2) clearly show that
48
49 omission of seasonality (models x.4) leads to a drastic reduction in R^2 for all functional
50
51 groups of invertebrates. On the other hand, omission of depth dependence (models x.5) or
52
53 nonlinearity of increase after a flood (models x.6) led to similarly good fits (inclusion of
54
55 depth dependence was better for scrapers and predators, inclusion of nonlinearity of increase
56
57 was better for total invertebrates and collector-gatherers). Omission of both effects (models
58
59 x.7) did not lead to satisfying behaviour. As the estimated parameter values for depth
60

1
2 dependence did not seem realistic and estimation of depth dependence seems to be critical
3
4 from just two sites of the same river with only small differences in depth, we selected the
5
6 models x.5 that interpreted the data with the nonlinear increase term after floods.
7
8

9
10 Figure 3 illustrates the results of the models x.5 ($x = 2, 3, 4$ and 5) compared to the
11
12 measured data from both sites.
13
14
15
16

17 5. DISCUSSION

18
19
20 The nonlinear regression models presented in the previous section differ in accuracy (R^2),
21
22 complexity and the number of data points used to derive the models. The algae models are
23
24 based on data sampled from eight sites located in three rivers ($n=286$) while the derivation of
25
26 the invertebrate models relied on data from only two sites at one river (Sihl) ($n=86$). The
27
28 results of the periphyton model fit the data surprisingly well (see Figure 2). Only two
29
30 parameters were fitted for a joint calibration to all eight data sets. This strongly supports the
31
32 chosen model structure. On the other hand, four parameters had to be fitted for each of the
33
34 four models of total invertebrates, scrapers, collector-gatherers, and predators at only two
35
36 sites at the same river (see Figure 3). This leads to a much weaker confidence in the
37
38 predictive capabilities of these models. The poorer performance of the scraper model as
39
40 compared to the other models is reflected by wider 90% prediction uncertainty bands that
41
42 extend nearly down to zero over the complete simulation period.
43
44
45
46
47
48

49
50 The quality of fit quantified by R^2 values was only slightly higher for the best non-linear
51
52 regression models as compared the best linear regression models. This shows that we cannot
53
54 considerably improve the quality of the fit with the nonlinear dependence formulation. The
55
56 reason for formulating nonlinear models was to avoid an unreasonable extrapolation
57
58 behaviour of the linear models. Extrapolating the linear models can lead to negative or
59
60

1
2 arbitrarily large predictions. Both of these behaviours are excluded by our formulation of the
3
4 nonlinear models.
5

6
7 The low variation in grain size across sites precluded estimation of the model parameter
8
9 k_{d50} characterizing decrease of biomass densities with decreasing grain size. Therefore, this
10
11 parameter was estimated from the literature to be 0.2 m (Biggs & Price 1987, Quinn &
12
13 Hickey 1990). Additionally, the maximum biomass density achieved under non-limiting
14
15 conditions for long times after a flood, $\overline{B_{\max}}$, was difficult to fit, since longer periods without
16
17 flood disturbances did not occur during the sampling period with the exception of the
18
19 Garonne river. Therefore, this parameter also had to be chosen based on the literature
20
21 (Yoshimura et al., 2006).
22
23
24
25
26

27 The model structure selection process based on the remaining parameters describing the
28
29 increase in biomass density after a flood, seasonal variation, and dependence on flow velocity
30
31 and water depth led to very different results for periphyton than for invertebrates. For
32
33 periphyton it led to the exclusion of a significant seasonal variation, a linear initial increase of
34
35 biomass with time after a flood, and a significant dependence on flow velocity. On the other
36
37 hand, seasonality is a dominant explaining variable for invertebrate biomass density and there
38
39 seems to be a strong nonlinearity of increase in time after a flood.
40
41
42
43

44 The absence of a strong seasonal variation of periphyton density seems to be a
45
46 surprising result, as the seasonal component in our simple model mainly represents the effect
47
48 of light and temperature on algal biomass. However, this finding is in agreement with earlier
49
50 results of a mechanistic model (Uehlinger et al., 1996). It seems that adaptation of
51
52 chlorophyll content and species composition of the benthic periphyton biofilm can
53
54 compensate for most of the light and temperature dependence observed for individual species.
55
56 The dependence on flow velocity may still contain some confounding with water depth and it
57
58 would be very interesting to separate those two effects. However, more data from sites with
59
60 considerable differences in flow velocity and water depth would be required to do this.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Due to their immobility, periphyton are more susceptible to floods compared to invertebrates which can move to more stable refuges (e.g. river bed interstitial, side braids, low-velocity areas around stable boulders) during high stage (Quinn & Hickey 1990). The regression analysis indicates that for periphyton, the best predictor is “time since the last bed-moving flood” (Δt_{flood}), while invertebrates (and most of their functional feeding groups) are more strongly controlled by seasonal effects. This is reflected in the nonlinear invertebrate models by the value of the parameter b smaller than unity that describes a faster recovery from the flood-induced depletion of invertebrates as compared to the linear recovery of periphyton (compare Figs. 2 and 3). In contrast to periphyton, invertebrates can have a more complicated life cycle (larvae, imago, adults) with possibly varying food and habitat preferences. This makes it more difficult to get good predictions for invertebrates with a simple non-linear regression model. This is also a significant problem for more complicated dynamic functional group models (Schuwirth et al., 2007). In our simple nonlinear regression approach, the life stages of invertebrates are aggregated into the seasonal effect described by the model.

The relationships found with the nonlinear regression approach can stimulate formulation of detailed mechanistic models of the benthos community such as those of Boulêtreau et al (2006) and Schuwirth et al (2007). The dominance of time since the last flood as an explaining variable for periphyton suggests the necessity of a careful formulation of flood-induced detachment processes and subsequent recovery by growth. Unless light, low temperatures and nutrients are significantly limiting (which is not the case for the sites studied in this paper), these factors seem to be of minor importance for a simple periphyton model for Swiss midland rivers. Nevertheless, these factors must be kept in mind when designing a model to be applied to different climatic regimes and with smaller nutrient loads or higher turbidity. For the invertebrate models, at least seasonally varying or temperature

1
2 dependent growth rates should be formulated, and the model should contain a higher relative
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
colonization rate after floods than the periphyton model.

The ratio of primary to secondary producer biomass estimated by the model can be compared to values predicted by theoretical concepts (e.g., Vannote et al 1980) and used for the evaluation of an expected ecosystem state. Moreover, the estimated biomass of the functional feeding groups can illuminate dominant pathways of nutrient cycling in a particular river reach (Yoshimura et al 2006, Merritt et al 1999, Klemm et al 2003, Böhmer et al 2000). For example, to assess habitat stability, Yoshimura et al (2006) propose to calculate the ratio of the more flood susceptible scrapers and collector-filterers to shredders and collector-gatherers. They recommend using abundances, but similar results can be expected when biomasses are used instead. Functional feeding groups emphasize the multiple linkages that exist between food resources and the ability of invertebrates to successfully acquire these resources (Cummins et al. 1981, Merritt et al. 1999, Barbour et al. 2001). Thus, function-based metrics are more directly related to ecosystem integrity than solely taxonomic composition (Yoshimura et al. 2006).

Our proposed models have the potential to support decision-making in the context of river rehabilitation, since periphyton and invertebrates play a key role in river ecology by serving as food for fish and controlling decomposition. Predictions of the response of these organisms to management actions can help to guide the selection of the most appropriate stream reaches and site-specific rehabilitation measures. While grain size and seasonal effects are usually not changed by rehabilitation measures, the hydraulic conditions (velocity, depth) usually are. In previous papers (Schweizer et al 2007a, 2007b) we developed a relatively simple hydraulic-morphological model to predict the hydraulic conditions after measures such as river widening. The major hydraulic responses of widening are an increased wetted perimeter, a lower mean water depth and flow velocity, and a higher spatial variability of depth and velocity. The simple benthic community models discussed in this

1
2 paper would predict a higher periphyton biomass density due to the decreasing flow velocity.
3
4 In addition, due to the increased wetted perimeter, there will be more habitat area available
5
6 per unit river length for both periphyton and invertebrates.
7
8
9

10 11 **6. SUMMARY AND CONCLUSIONS**

12
13
14
15 Simple nonlinear regression models were developed for describing the biomass of periphyton
16
17 and benthic invertebrate functional feeding groups in rivers as a function of time since the last
18
19 bed-moving flood, mean water depth, grain size, mean flow velocity, and season (time within
20
21 the year). The models were calibrated using periphyton data from 8 sites in 3 rivers and
22
23 invertebrate feeding group data from 2 sites in one river. The statistical approach made it
24
25 much easier to derive relationships between biomass densities of functional groups of the
26
27 benthos community across different rivers and sites than would have been possible with
28
29 mechanistic models. The results of sensitivity analyses, the model structure selection process,
30
31 and comparisons of model results with data lead to the following conclusions:
32
33
34
35

- 36
37 • Considering the diversity of data sets and the simplicity of the models, the models
38
39 lead to a remarkably good agreement with time series of measurements. Due to the
40
41 larger data set available, this is particularly true for the periphyton model.
42
43
- 44
45 • The major influence factors for periphyton were identified to be time since the last
46
47 bed-moving flood and mean flow velocity. No significant seasonal effects could be
48
49 identified. In contrast to this result, seasonally varying influence factors or seasonal
50
51 effects of changing life stages were identified to be important factors influencing total
52
53 invertebrate and invertebrate functional feeding group biomass. Recovery after flood-
54
55 induced disturbance events was identified to be significantly faster for invertebrates
56
57 than for periphyton.
58
59
60

- The small number and simple nature of the considered influence factors makes the model an easily applicable tool for predicting the effect of rehabilitation measures on the benthic community.
- The model was derived with as many data sets as were available. Nevertheless a better support by data from additional rivers is necessary to test and improve its universality.

The suggested simple benthic community models seem to be useful for roughly estimating the effect of river rehabilitation measures on the benthic community. Furthermore, they support the development of more detailed mechanistic model of benthic community dynamics. More and longer data sets of rivers of different characteristics would be extremely useful for improving the development of both model types.

ACKNOWLEDGEMENTS

This study was supported by the Rhone-Thur project, which was initiated and is funded by the Swiss Federal Office for Water and Geology (BWG) (now BAFU), the Swiss Federal Institute for Environmental Science and Technology (Eawag) and the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). For stimulating discussions, comments, helpful advices and for sharing valuable datasets, we thank the Rhone-Thur project partners (P. Baumann, K. Tockner) and N. Lamouroux, C. Robinson, C. Yoshimura, S. Boulétreau, D. Arscott, M. Scarsbrook, V. Acuña, H.-L. Morf, J. Hürlimann, F. Elber, K. Niederberger, P. Burgherr and E. Meyer.

REFERENCES

- Améziane T, Garabétian F, Dalger D, Sauvage S, Dauta A and Capblancq J. 2002. Epilithic biomass in a large gravel-bed river (the Garonne, France): a manifestation of eutrophication? *River Research and Applications* **18**: 343-354.
- Barbour M T, Geristen J, Snyder B D, Stribling J B. 2001. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish. EPA, Washington DC, p1-339.
- Biggs B J F & Price G M. 1987. A survey of filamentous algal proliferations in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **21**: 175-181.
- Böhmer J, Rawer-Jost C and Kappus B. 2000. Ökologische Fließgewässerbewertung. Biologische Grundlagen und Verfahren - Schwerpunkt Makrozoobenthos. In: Handbuch Angewandte Limnologie.
- Borsuk M E, Stow C A, Higdon D and Reckhow K H. 2001. A Bayesian hierarchical model to predict benthic oxygen demand from organic matter loading in estuaries and coastal zones. *Ecological Modelling* **143**: 165-181.
- Borsuk M E, Reichert P, Peter A, Schager E, Burkhardt-Holm P. 2006. Assessing the decline of brown trout (*Salmo trutta*) in Swiss rivers using a Bayesian probability network. *Ecological Modelling*, **192**: 224-244.
- Boulétreau S, Garabétian F, Sauvage S and Sanchez-Pérez J-M. 2006. Assessing the importance of a self-generated detachment process in river biofilm models. *Freshwater Biology* **51(5)**: 901-912.
- Box G E P & Cox D R. 1964. An analysis of transformations. *Journal of the Royal Statistical Society Series B*, 211-252.
- Box G E P & Cox D R. 1982. An analysis of transformations revisited, rebutted. *Journal of the American Statistical Association* **77(377)**: 209-210.

- 1
2 Bretschneider H & Schulz A. 1985. Anwendung von Fließformeln bei naturnahem
3
4 Gewässerausbau. *Schriftenreihe des deutschen Verbandes für Wasserwirtschaft und*
5
6 *Kutlurbau e.V. Heft 2*. Verlag Paul Parey, Hamburg, Berlin.
- 7
8
9 Cummins K W, Klug M J, Ward G M, Spengler G L, Speaker R W, Ovink R W, Mahan D C
10
11 and Petersen R C. 1981. Trends in particulate organic matter fluxes, community processes
12
13 and macroinvertebrate functional feeding groups along a Great Lakes Drainage Basin river
14
15 continuum. *Verh. Internat. Verein. Limnol.* **21**: 841-849.
- 16
17
18 Elber F, Hürlimann J and Niederberger K. 1992. Biologische Begleitung der Schwallversuche
19
20 vom Sommer 1990 in der Sihl. *Wasser, Energie, Luft* **84** (3/4): 42-50.
- 21
22
23 Elber F, Hürlimann J and Niederberger K. 1996. Algenmonitoring als Grundlage für das
24
25 Abflussmanagement in der Sihl. *Wasser, Energie, Luft* **88** (3/4): 55-62.
- 26
27
28 Gevrey M, Dimopoulos I and Lek S. 2003. Review and comparison of methods to study the
29
30 contribution of variables in artificial neural network models. *Ecological Modelling* **160**:
31
32 249-264.
- 33
34
35 Hostmann M, Borsuk M, Reichert P, Truffer B. 2005. Stakeholder values in decision support
36
37 for river rehabilitation. *Large Rivers* **15**(1-4) *Arch. Hydrobiol. Suppl.* **155**/1-4: 491-505.
- 38
39
40 Klemm D J, Blocksom K A, Fulk F A, Herlihy A T, Hughes R M, Kaufmann P R, Peck D V,
41
42 Stoddard J L, Thoeny W T and Griffith M B. 2003. Development and evaluation of a
43
44 macroinvertebrate biotic integrity index (MBII) for regionally assessing Mid-Atlantic
45
46 Highlands streams. *Environmental Management* **31**: 656-669.
- 47
48
49 Lamouroux N, Doledec S, Gayraud S. 2004. Biological traits of stream macroinvertebrate
50
51 community: effects of microhabitat, reach, and basin filters. *J. N. Am. Benthol. Soc.* **23**(3):
52
53 449-466.
- 54
55
56 McIntire C D. 1973. Periphyton dynamics in laboratory streams: a simulation model and its
57
58 implications. *Ecological Monographs* **43**: 399-420.
- 59
60

- 1
2 Merritt R W, Higgins M J, Cummins K W and Vandeneden B. 1999. The Kissimmee River-
3
4 Riparian Marsh Ecosystem, Florida. Seasonal differences in invertebrate functional
5
6 feeding group relationships. In *Invertebrates in Freshwater Wetlands of North America:
7
8 Ecology and Management*. Edited by Darold P Batzer D P, Rader R B, and Wissinger S A,
9
10 John Wiley & Sons, Inc.
11
12
- 13
14 Park Y-S, Céréghino R, Compin A and Lek S. 2003. Applications of artificial neural
15
16 networks for patterning and predicting aquatic insect species richness in running waters.
17
18 *Ecological Modelling* **160**: 265-280.
19
20
- 21
22 Power M E, Dudley T L, Cooper S D. 1989. Grazing catfish, fishing birds, and attached algae
23
24 in a Panamanian stream. *Environmental Biology of Fishes* **26**:285-294.
25
26
- 27
28 Power M E, Sun A, Parker G, Dietrich W E, and Wootton J T. 1995. Hydraulic food-chain
29
30 models. An approach to the study of food-web dynamics in large rivers. *Bioscience* **45**:
31
32 159-167.
33
- 34
35 Quinn J M & Hickey C W. 1990. Magnitude of effects of substrate particle size, recent
36
37 flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers.
38
39 *New Zealand Journal of Marine and Freshwater Research* **24**: 411-427.
40
- 41
42 Reichert P, Borchardt D, Henze M, Rauch W, Shanahan P, Somlyody L and Vanrolleghem P.
43
44 2001. River Water Quality Model no.1 (RWQM1): II. Biochemical process equations.
45
46 *Water Science and Technology* **43**(5): 11-30.
47
48
- 49
50 Reichert P, Borsuk M, Hostmann M, Schweizer S, Spörri C, Tockner K and Truffer B. 2007.
51
52 Concepts of decision support for river rehabilitation. *Environmental Modelling and
53
54 Software* **22**: 188-201.
55
- 56
57 Schuwirth N., Kühni M, Schweizer S, Uehlinger U and Reichert P. 2007. A mechanistic
58
59 model of benthos community dynamics in the River Sihl, Switzerland. *Submitted to
60
Freshwater Biology*.

- 1
2 Schweizer S, Borsuk M, Jowett I, Reichert P. 2007a. Predicting joint frequency distributions
3 of depth and velocity for instream habitat assessment. *River Research and Applications*, in
4 press.
5
6
7
8
9 Schweizer S, Borsuk M, Reichert P. 2007b. Predicting the hydraulic and morphological
10 consequences of river rehabilitation. *River Research and Applications*, in press.
11
12
13
14 Spörri C, Borsuk M, Peters I and Reichert P. 2007. The economic impacts of river
15 rehabilitation: a regional input-output analysis. *Ecological Economics*, in press.
16
17
18
19 Uehlinger U. 1991. Spatial and temporal variability of the periphyton biomass in a prealpine
20 river (Necker, Switzerland). *Arch. Hydrobiol.* **123**(2): 219-237.
21
22
23
24 Uehlinger U, Bühner H and Reichert P. 1996. Periphyton dynamics in a floodplain prealpine
25 river: evaluation of significant processes by modelling. *Freshwater Biology* **36**: 249-263.
26
27
28
29 Vannote R L, Minshall G W, Cummins K W, Sedell J R and Cushing C E. 1980. The river
30 continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130-137.
31
32
33
34 Yoshimura C, Tockner K, Omura T and Moog O. 2006. Species diversity and functional
35 assessment of macroinvertebrate communities in Austrian rivers. *Limnology* **7** (2): 63-74.
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table 1: Summary of site characteristics. (DIN= dissolved inorganic nitrogen = $\sum\text{NO}_3\text{-N}$, $\text{NO}_2\text{-N}$, $\text{NH}_4\text{-N}$; SRP = soluble reactive phosphorus)

Parameter/ site name	Necker Aachsäge main channel	Necker Aachsäge side channel	Necker Aachsäge gravel bar	Necker Down- stream	Sihl Up- stream	Sihl Down- stream	Garonne Aouach	Garonne Gagnac
Catchment Area (km ²)	88	88	88	126	na	na	56000	56000
Height a.s.l. (m)	607	607	607	559	485	442	na	na
Mean Discharge (m ³ /s)	3.4	3.4	3.4	4.6	3 ⁺	3 ⁺	113	159
Slope (-)	na	na	na	0.006	na	na	0.005	0.005
Grain Size (m)	0.08	0.08	0.08	0.05	0.22	0.16	0.12	0.12
Mean Velocity (ms ⁻¹)	0.8	0.5	0.5	0.7	0.63*	0.5	1	1
Mean Depth (m)	0.2	0.2	0.1	0.4	0.4	0.5	0.5	0.5
Mean Fr (-)	0.6	0.3	0.4	0.3	0.4	0.2	0.5	0.5
Mean Temperature (Winter) (°C)	2.1	2.1	2.1	2.3	1	1	8.1	8.1
Mean Temperature (Summer) (°C)	14	14	14	15.7	15	15	20.0	20.0
Shading by riparian vegetation (%)	35%	0%	5%	0%	0%	0%	na	na
DIN (mg l ⁻¹)	1.22	1.22	1.22	1.28	0.82	0.82	0.74	1.59
SRP (µg l ⁻¹)	38	38	38	25	50	50	9	85
Number of samples	29	29	29	46	43	43	33	34

⁺ Artificial flow regime

* The reported value of 0.8 m/s had to be reduced to guarantee compatibility with the downstream site with approximately the same width and discharge.

na – data not available

Table 2: Summary of influence factors used to derive models for periphyton and invertebrates. DIN = Dissolved inorganic nitrogen ($\sum\text{NO}_3\text{-N}$, $\text{NO}_2\text{-N}$, $\text{NH}_4\text{-N}$)
SRP = Soluble reactive phosphorus

Influence Factor	Units	Minimum	Mean	Maximum
Julian Day	(-)	1 (1 st January)	169 (18 th June)	365 (31 st December)
Month	(-)	1 (January)	7 (July)	12 (December)
Season	(-)	Spring	Summer/Fall	Winter
Time since last flood with bed movement	(d)	0	95	411
Time since last minor flood (exceeding twice the mean discharge)	(d)	0	8	35
Temperature of the last 14 or 30 days	(°C)	0.3	10.7	24.5
Seasonal Temperature	(°C)	1.0	10.8	20.0
Mean Discharge	(m ³ /s)	3.0	34.6	159.0
Flow Velocity	(m/s)	0.5	0.7	1.0
Water Depth	(m)	0.1	0.4	0.5
Froude N ^o	(-)	0.3	0.4	0.6
Median Grain Size	(m)	0.05	0.12	0.22
DIN	(mg/l)	0.7	1.1	1.6
SRP	(µg/l)	9	42	85
Catchment Area	(km ²)	88		56000

Table 3: Parameter estimates of base model (x.1), of models used for sensitivity analysis of fixed parameters (x.2 and x.3), and for simplified models used for model structure selection (x.4 to x.9 (see text for additional explanation)). The values of fitted parameters are indicated in bold; fixed parameter values are in standard style; and parameter values that were fixed to yield omission of a term are in italics. n is the number of fitted model parameters. Finally selected models are indicated with bold model identifiers in the second column.

	model	$\overline{B_{\max}}$	$\overline{k_B}$	k_{d50}	$\Delta t_{\text{jul}}^{\max}$	α	γ	δ	b	n	R ²
periphyton	1.1	1500	22.6	0.2	220.0	0.056	0.34	2.96	0.89	6	0.595
	1.2	3000	31.9	0.2	235.9	0.097	0.40	3.36	0.82	6	0.611
	1.3	1500	28.3	0.4	129.8	0.016	0.55	2.46	0.94	6	0.577
	1.4	1500	23.8	0.2	<i>250</i>	<i>0</i>	0.29	2.97	0.87	4	0.594
	1.5	1500	21.8	0.2	218.5	0.047	<i>0</i>	3.11	0.89	5	0.594
	1.6	1500	26.4	0.2	125.8	0.100	3.24	<i>0</i>	0.50	5	0.382
	1.7	1500	16.8	0.2	219.3	0.079	0.35	3.07	<i>1</i>	5	0.593
	1.8	1500	16.5	0.2	<i>250</i>	<i>0</i>	<i>0</i>	3.22	<i>1</i>	2	0.590
	1.9	1500	17.0	0.2	<i>250</i>	<i>0</i>	0.27	3.10	<i>1</i>	3	0.591
total invertebrates	2.1	150	4.47	0.2	257.9	0.781	1.85	<i>0</i>	0.63	5	0.726
	2.2	300	5.73	0.2	257.1	0.788	2.40	<i>0</i>	0.59	5	0.732
	2.3	150	5.05	0.4	257.9	0.780	1.11	<i>0</i>	0.64	5	0.727
	2.4	150	9.11	0.2	<i>250</i>	<i>0</i>	2.65	<i>0</i>	0.54	3	0.356
	2.5	150	2.26	0.2	257.1	0.788	<i>0</i>	<i>0</i>	0.57	4	0.713
	2.6	150	3.57	0.2	255.1	0.793	3.53	<i>0</i>	<i>1</i>	4	0.693
	2.7	150	0.45	0.2	243.8	0.887	<i>0</i>	<i>0</i>	<i>1</i>	3	0.607
scrapers	3.1	25	5.45	0.2	250.9	0.878	5.02	<i>0</i>	0.58	5	0.304
	3.2	50	7.55	0.2	249.9	0.884	5.77	<i>0</i>	0.44	5	0.303
	3.3	25	5.91	0.4	251.0	0.877	4.15	<i>0</i>	0.61	5	0.306
	3.4	25	9.67	0.2	<i>250</i>	<i>0</i>	5.93	<i>0</i>	0.96	3	0.055
	3.5	25	0.84	0.2	250.5	0.887	<i>0</i>	<i>0</i>	0.27	4	0.261
	3.6	25	5.22	0.2	253.6	0.862	5.77	<i>0</i>	<i>1</i>	4	0.296
	3.7	25	0.06	0.2	230.5	0.969	<i>0</i>	<i>0</i>	<i>1</i>	3	-0.031
Collect.-gatherers	4.1	100	0.80	0.2	248.5	0.770	-0.61	<i>0</i>	0.61	5	0.637
	4.2	200	0.86	0.2	248.3	0.772	-0.45	<i>0</i>	0.60	5	0.639
	4.3	100	0.96	0.4	248.3	0.770	-1.20	<i>0</i>	0.62	5	0.641
	4.4	100	1.57	0.2	<i>250</i>	<i>0</i>	-0.25	<i>0</i>	0.47	3	0.338
	4.5	100	1.01	0.2	248.6	0.768	<i>0</i>	<i>0</i>	0.62	4	0.636
	4.6	100	1.20	0.2	243.0	0.808	2.90	<i>0</i>	<i>1</i>	4	0.560
	4.7	100	0.26	0.2	237.5	0.867	<i>0</i>	<i>0</i>	<i>1</i>	3	0.535
predators	5.1	30	1.64	0.2	277.8	0.816	4.16	<i>0</i>	0.70	5	0.578
	5.2	60	2.60	0.2	276.4	0.823	5.47	<i>0</i>	0.69	5	0.602
	5.3	30	1.78	0.4	278.0	0.814	3.27	<i>0</i>	0.70	5	0.569
	5.4	30	2.15	0.2	<i>250</i>	<i>0</i>	4.79	<i>0</i>	0.68	3	0.286
	5.5	30	0.28	0.2	271.8	0.843	<i>0</i>	<i>0</i>	0.59	4	0.515

1											
2	5.6	30	0.98	0.2	274.9	0.826	4.81	0	1	4	0.565
3	5.7	30	0.06	0.2	258.8	0.919	0	0	1	3	0.476
4											
5											
6											
7											
8											
9											
10											
11											
12											
13											
14											
15											
16											
17											
18											
19											
20											
21											
22											
23											
24											
25											
26											
27											
28											
29											
30											
31											
32											
33											
34											
35											
36											
37											
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											
48											
49											
50											
51											
52											
53											
54											
55											
56											
57											
58											
59											
60											

For Peer Review

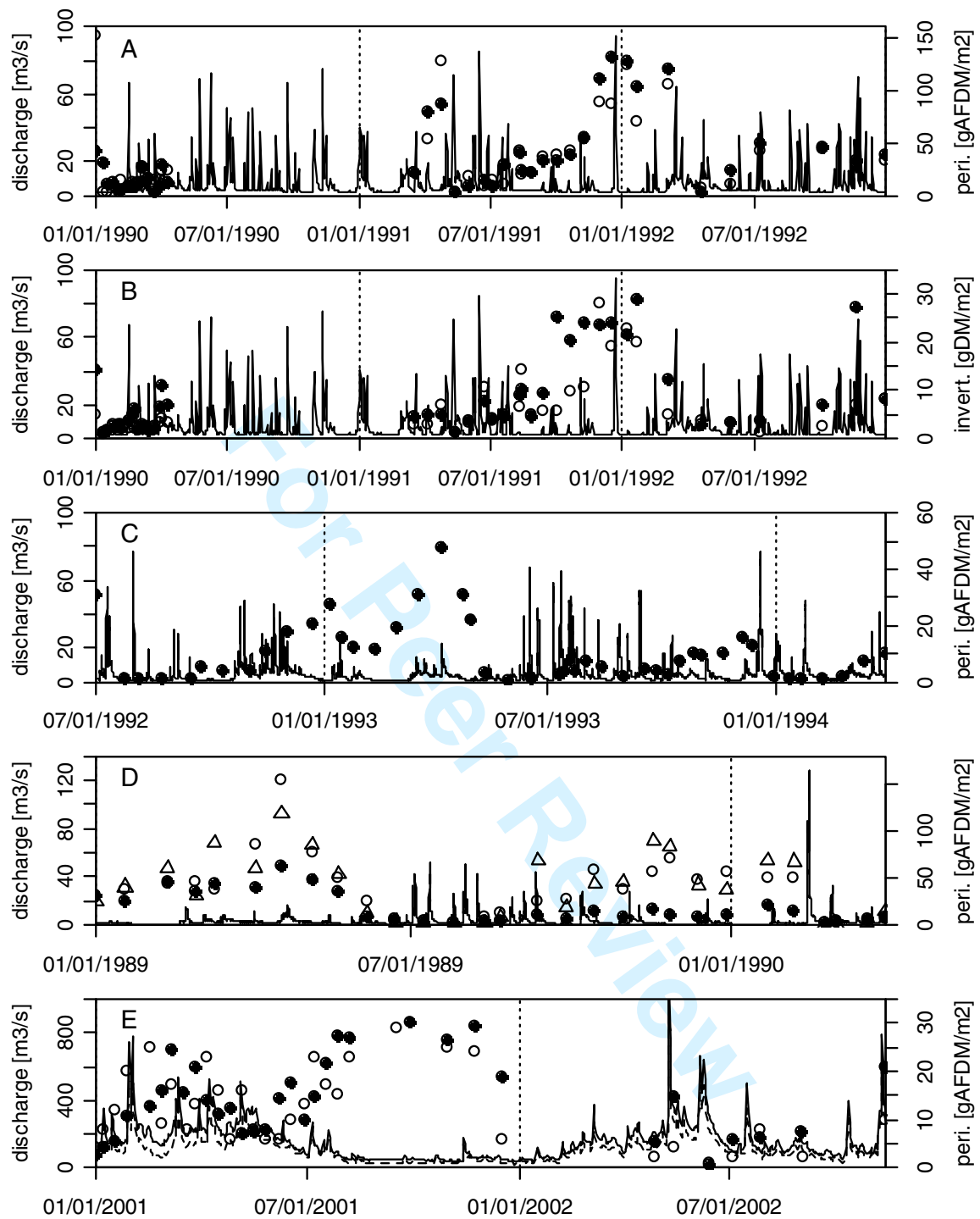


Figure 1: Discharge time series (solid and dashed lines) and measured functional group biomass (markers) for the study sites. Periphyton (AFDM; panel A) and benthic invertebrate biomass (panel B) for the upstream (solid circles) and downstream (circles) sites of the River Sihl. Periphyton biomass for the sites “Downstream” (panel C) and “Aachsäge” (panel D; solid circles: main channels; circles: gravel bar; and side channel: triangles) at the Necker

1
2 River, and for the the sites “Aouach” (solid circles) and “Gagnac” (circles) at the Garonne
3
4 River (panel E). The solid line in panel E represents the discharge at Aouach, the dashed line
5
6 the discharge at Gagnac.
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Peer Review

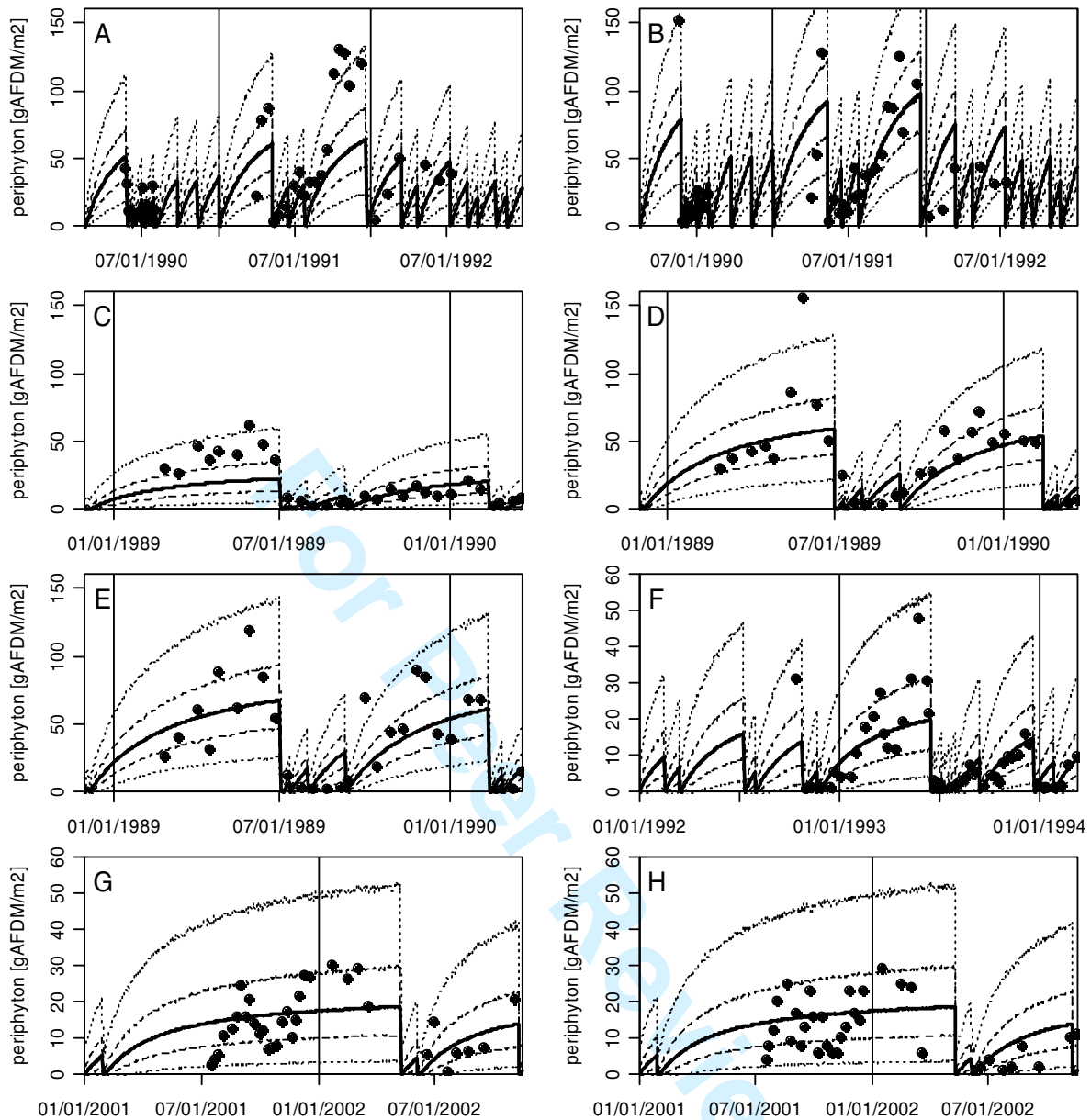


Figure 2: Time series of results of model 1.8 and measured periphyton biomass (solid circles) for all study sites. The solid lines represent the best estimates, the dashed lines bound the 50% and the outer dotted lines the 90% uncertainty intervals of the predictive distributions and the symbols represent measured data. A: Sihl upstream site. B: Sihl downstream site. C: Necker Aachsäge main channel. D: Necker Aachsäge gravel bar. E: Necker Aachsäge side channel. F: Necker downstream site. G: Garonne Gagnac. H: Garonne Aouach.

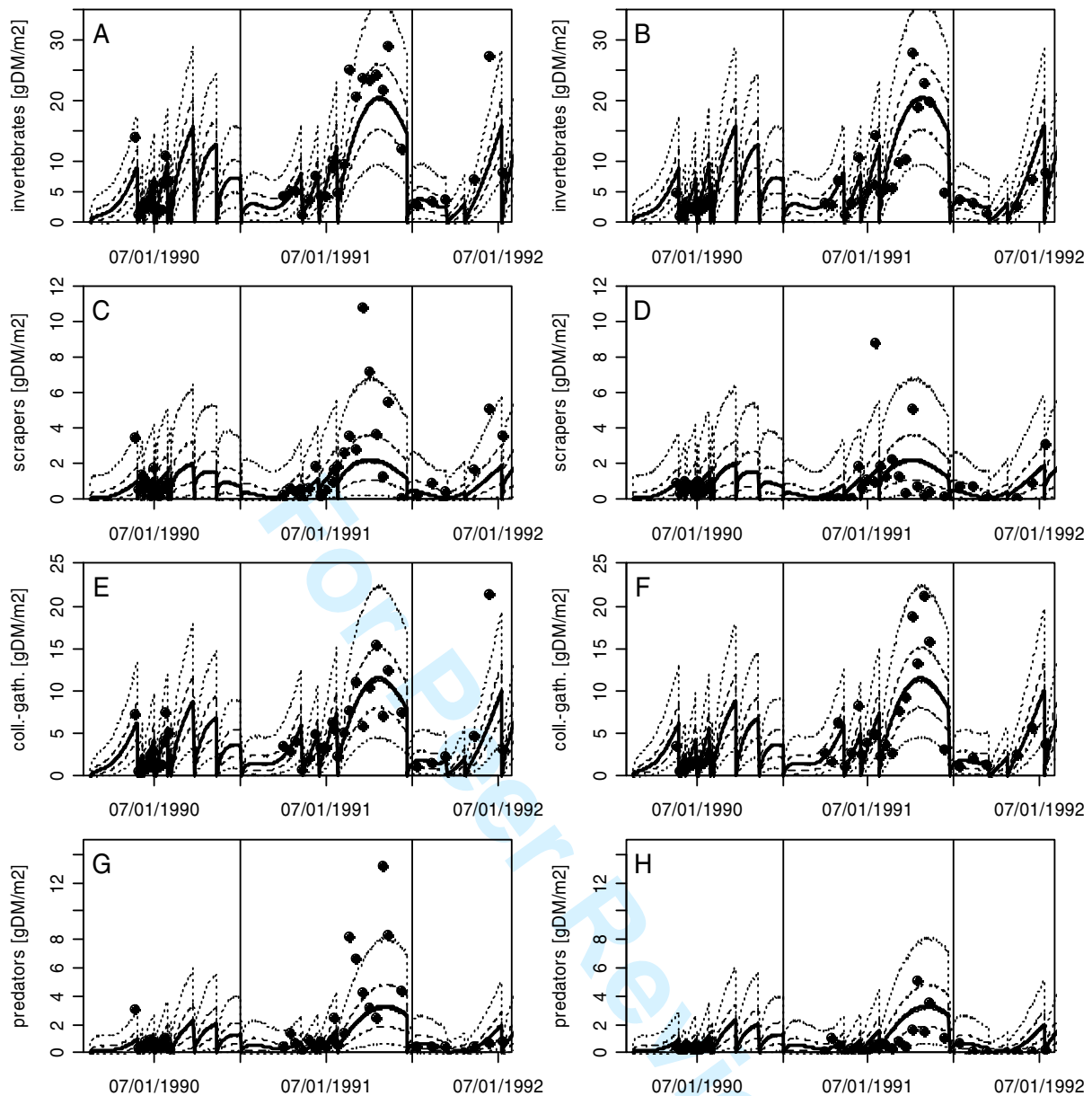


Figure 3: Time series of results of invertebrate models and data from the Sihl River. The solid lines represent the best estimates, the dashed lines bound the 50% and the outer dotted lines the 90% uncertainty intervals of the predictive distributions and the solid circles represent measured data. Left column: upstream site. Right column: downstream site. Top row (panels A and B): model 2.5 for total invertebrate biomass density. Second row (panels C and D): model 3.5 for scraper biomass density. Third row (panels E and F): model 4.5 for collector-gatherer biomass density. Bottom row (panels G and H): model 5.5 for predator biomass density.

APPENDIX

Uncertainty of model parameters and correlation between model parameters (sd = standard error, for abbreviation of model parameters see chapter 3.2). The standard deviations of the error term in equation (5) were $1.63 \text{ (gAFDM/m}^2\text{)}^{0.3}$ for periphyton, $0.75 \text{ (gDM/m}^2\text{)}^{0.3}$ for total invertebrates, $0.94 \text{ (gDM/m}^2\text{)}^{0.3}$ for scrapers, $0.81 \text{ (gDM/m}^2\text{)}^{0.3}$ for collector-gatherers, and $0.75 \text{ (gDM/m}^2\text{)}^{0.3}$ for predators.

		Estimate	sd	Coefficient of correlation r							
				\overline{B}_{\max}	\overline{k}_B	k_{d50}	$\Delta t_{\text{jul}}^{\max}$	α	γ	δ	b
Periphyton Model 1.8	B_{\max}	1500	300	1	0	0	-	-	-	0	-
	k_B	16.5	2.2	0	1	0	-	-	-	0.84	-
	k_{d50}	0.2	0.04	0	0	1	-	-	-	0	-
	$\Delta t_{\text{jul}}^{\max}$	0	-	-	-	-	-	-	-	-	-
	α	0	-	-	-	-	-	-	-	-	-
	γ	0	-	-	-	-	-	-	-	-	-
	δ	3.22	0.11	0	0.84	0	-	-	-	1	-
	b	1	-	-	-	-	-	-	-	-	-
Total invertebrates Model 2.5	B_{\max}	150	30	1	0	0	0	0	-	-	0
	k_B	2.26	0.52	0	1	0	0.55	-0.31	-	-	-0.96
	k_{d50}	0.2	0.04	0	0	1	0	0	-	-	0
	$\Delta t_{\text{jul}}^{\max}$	257.1	6.2	0	0.55	0	1	-0.33	-	-	-0.46
	α	0.79	0.06	0	-0.31	0	-0.33	1	-	-	0.29
	γ	0	-	-	-	-	-	-	-	-	-
	δ	0	-	-	-	-	-	-	-	-	-
	b	0.57	0.06	0	-0.96	0	-0.46	0.29	-	-	1
Scrapers Model 3.5	B_{\max}	25	5	1	0	0	0	0	-	-	0
	k_B	0.84	0.33	0	1	0	0.55	-0.30	-	-	-0.93
	k_{d50}	0.2	0.04	0	0	1	0	0	-	-	0
	$\Delta t_{\text{jul}}^{\max}$	250.5	11.5	0	0.55	0	1	-0.28	-	-	-0.41
	α	0.89	0.13	0	-0.30	0	-0.28	1	-	-	0.26
	γ	0	-	-	-	-	-	-	-	-	-
	δ	0	-	-	-	-	-	-	-	-	-
	b	0.27	0.11	0	-0.93	0	-0.41	0.26	-	-	1
Collector-Gatherers Model 4.5	B_{\max}	100	20	1	0	0	0	0	-	-	0
	k_B	1.01	0.25	0	1	0	0.51	-0.34	-	-	-0.95
	k_{d50}	0.2	0.04	0	0	1	0	0	-	-	0
	$\Delta t_{\text{jul}}^{\max}$	248.6	7.2	0	0.51	0	1	-0.30	-	-	-0.41
	α	0.77	0.07	0	-0.34	0	-0.30	1	-	-	0.32
	γ	0	-	-	-	-	-	-	-	-	-
	δ	0	-	-	-	-	-	-	-	-	-
	b	0.62	0.07	0	-0.95	0	-0.41	0.32	-	-	1
Predators Model 5.5	B_{\max}	30	6	1	0	0	0	0	-	-	0
	k_B	0.28	0.12	0	1	0	0.58	-0.22	-	-	-0.96
	k_{d50}	0.2	0.04	0	0	1	0	0	-	-	0
	$\Delta t_{\text{jul}}^{\max}$	271.8	9.9	0	0.58	0	1	-0.28	-	-	-0.50
	α	0.84	0.08	0	-0.22	0	-0.28	1	-	-	0.22
	γ	0	-	-	-	-	-	-	-	-	-
	δ	0	-	-	-	-	-	-	-	-	-
	b	0.59	0.11	0	-0.96	0	-0.50	0.22	-	-	1

- = model parameter not estimated