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Feature Article

Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl)

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Abstract. We investigated the effects of an experimental flood regime on periphyton and stream metabolism downstream of a large reservoir. Three floods took place in summer of 2000 and 2001 and two floods in summer of 2002. Residual flow in the River Spöl was $<2.5\ m^3 s^{-1}$. The experimental floods lasted 9 to 11 hours with peak flows ranging from 12 to 55 $m^3 s^{-1}$. Periphyton was collected in the River Spöl (impact site) and in a reference stream in 1999 (pre-flood) and before and after each flood from 2000 to 2002. We measured ecosystem metabolism with the single station diel oxygen method a few days before and after floods in the River Spöl. Floods temporarily reduced periphyton biomass, but the disturbance impact and recovery patterns were not uniform among floods, thus resulting in high inter-annual variation in seasonal biomass patterns. The average periphyton biomass in the River Spöl even increased after a transient reduction in 2000. A principal component analysis indicated a persistent shift in the structure of the diatom community at the impact site. The floods reduced gross primary production and to minor extent ecosystem respiration, resulting in a transient decline in the P/R ratio. However, ecosystem metabolism recovered relatively fast. The new flow regime increased ecosystem dynamics, but it may take several years until the autotrophic energy base becomes adapted to the new and more dynamic flow regime.

Key words. Flow regime; disturbance; ecosystem metabolism; river management.

Introduction

Flow, the most important factor influencing the structure and function of lotic ecosystems, has been subject to human modifications through urbanization, flood control by dikes, storage and abstraction of water for irrigation, drinking water, and power production (Dynesius and Nilsson, 1994; Poff et al., 1997). Dams are ubiquitous structures on many flowing waters that alter flow and temperature regimes, hydraulics, the stability and availability of substrata, channel morphology, and the riparian vegetation, and, as a consequence, the structure of benthic and fish communities (Blinn and Cole, 1990; Cazaubon and Giudicelli, 1999; Rader and Belish, 1999; Stromberg and Patten, 1990; Ward and Stanford, 1983).

In the Swiss Alps, power production is the primary reason for water abstraction and transient water storage in reservoirs. Stream flow below abstraction sites and dams is greatly reduced or often lacking, although tributaries provide some water. Further downstream, the diversion of water to power plants usually results in a highly unnatural flow regime (hydro peaking). For example, operation of the large dam at Punt dal Gall (near the border of the

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Swiss National Park) has resulted in a minimal, almost constant, residual flow that lacks the power to entrain and transport coarse sediments. The low flow has allowed the riverbed to be clogged with fine sediments, which has impaired the natural reproduction of the brown trout population (Ortlepp and Mürle, 2003), and enhanced the formation of large pools upstream of lateral debris fans (Mürle et al., 2003). The constant and relative benign environment resulted in dense algal mats, extensive moss beds, and an invertebrate community highly atypical for an Alpine mountain river (Robinson et al., 2003 a, b). The power company, the Swiss National Park, and state authorities agreed in 1996 to study the possibility of improving habitat conditions below the dam by using artificial floods beginning in 2000 (Scheurer and Molinari, 2003).

In this paper, we focus on the effects of floods on periphyton below the dam of Punt dal Gall. Besides using the data in river management, the experiment also provided the opportunity to study the response of periphyton to a changing disturbance regime over a period of three years. Based on our studies of low elevation streams (Robinson et al., 2000; Uehlinger, 1991; Uehlinger et al., 1996), we hypothesized that the floods would result in a transient reduction in periphyton biomass. Further, we anticipated that implementing a more dynamic flow regime to a system that has been characterized by highly constant environmental conditions (constant flow, few floods, minor variation in nutrients and temperature) would be reflected in changes in the taxonomic composition of the periphyton community. To evaluate the influence of the floods, we started sampling the impacted river and an adjacent stream not affected by flow manipulations (control site) one year before the first experimental flood. The assessment of certain functional processes such as sediment respiration and ecosystem metabolism, however, began after the new flow regime had been implemented, and measuring ecosystem metabolism at the control site was not possible because of highly turbulent flow (high re-aeration).

Methods

Study sites

The Spöl valley is located in the central part of the inner Alps (E 10°11′22″, N 46°36′38″). The climate of the catchment is continental with relatively low precipitation and high seasonal temperature variation compared to the northern and southern front ranges of the Alps (Barry, 1992). Coniferous forests dominate the vegetation of the subalpine zone extending to an elevation between 2100 and 2200 m a.s.l. The middle and lower River Spöl is part of a complex hydroelectrical power plant scheme (Scheurer and Molinari, 2003). Below the Punt dal Gall dam, the river flows through a confined reach for about 5.7 km before it enters the reservoir of Ova Spin. The main study site is a 50 m long reach (Punt Periv) located about 2.3 km downstream of the dam of Punt dal Gall. This site has been sampled since May 1999. In 2001, two additional sites 0.15 and 1.2 km downstream of the dam also were included to study the longitudinal effects of the artificial floods (Jakob et al., 2003). With the completion of the dam in 1969, annual mean discharge was reduced from 8.6 to 1.0 m^3/s and hypolimnetic reservoir water became the primary water source, being released through a turbine located at the base of the dam.

Table 1. Catchment and site characteristics of the River Spöl and Val da l'Aqua stream.

Catchment	Spöl	Val da l'Aqua
Area at the study site (km^2)	286	4.3
Area between dam and study site (km^2)	6	–
Glacierized area (%)	1.0	0.2
Maximum elevation (m a.s.l.)	3302	3118
Study sites		
Elevation (m a.s.l.)	1660	1750
Channel slope (%)	1–2	5–6
Channel width (m)	10–18	3–7
Annual mean discharge (m^3s^{-1})	1.1	0.3
Dominant substrata	gravel – boulder bedrock	cobble – boulder

The control stream is an unregulated tributary (Val da l'Aqua) that flows into the Spöl about 0.8 km downstream of the main study reach. Primary water sources are groundwater, snowmelt and melt water from a small glacier. This system contrasts with the Spöl in some important aspects such as size, slope, and structure of the riparian zone (Table 1) and, thus, limits its use as a reference site for the River Spöl. Nevertheless, data from this site can be used to assess temporal patterns in the periphyton community under natural flow conditions (nival-alpine flow regime; Aschwanden and Weingartner, 1985). The reference and impact sites are both located in the subalpine forest. *Picea excelsa* and *Pinus mugo* are the predominant riparian tree species between the Punt dal Gall dam and Punt Periv. *Pinus mugo* dominates the riparian forest in Val da l'Aqua.

Experimental flooding

The use of water for artificial floods had to result in no loss in energy production. This was possible due to the favorable configuration of reservoirs, aqueducts, and power houses that allowed re-allocating water for power production and at the same time maintaining residual flow in the River Spöl (Scheurer and Molinari, 2003). Residual flow

Table 2. The flood regime of the River Spöl below the dam of Punt dal Gall from 2000–2002.

Year	Date	Peak flow m^3 s^{-1}	Duration hours
2000	15 June	16	10 (7h with $Q \geq 14$ m^3 s^{-1})
	5 July	42	11 (7h with $Q \geq 28$ m^3 s^{-1})
	10 August	12	9.5 (7h with $Q \geq 11$ m^3 s^{-1})
	13–16 October[a]	28	87 (9h with $Q \geq 20$ m^3 s^{-1})
2001	13 June	12	11 (7h with $Q \geq 11$ m^3 s^{-1})
	5 July	55	11 (7h with $Q \geq 30$ m^3 s^{-1})
	7 August	13	11 (7h with $Q \geq 12$ m^3 s^{-1})
2002	2 July	51	11 (4h with $Q \geq 29$ m^3 s^{-1})
	8 August	14	9 (4.5h with $Q > 12$ m^3 s^{-1})

[a] High flow release over the flood gates at the dam crest during and after a period of excessive precipitation.

was reduced during summer and a part of this water was released for 8 floods between 2000 and 2002 (Table 2). The experimental flood peaks were comparable to those before dam construction (Fig. 1A, B) but the duration of these floods was distinctly shorter (≤11 h). However, in October 2000, heavy precipitation filled the reservoir above storage capacity, resulting in a high flow period for 3 days to release the surplus water (Table 2).

Sampling and data evaluation

Field sampling began in May 1999, about 13 months before the first flood. Discharge data for the River Spöl at the gauging station at Punt dal Gall were provided by the Federal Office for Water and Geology (Fig. 1A, B). Discharge in Val da l'Aqua was measured on several occasions using the salt dilution method (Gordon et al., 1992). To estimate discharge between these measurements, we used the discharge record of the nearby Cluozza River and the linear relationship between the measured discharge data of both streams ($r^2 = 0.40$, $n = 12$, $p < 0.01$). Temperatures were recorded hourly at Val da l'Aqua and the main Spöl site (Punt Periv) since May 1999 using temperature loggers (Minilog, Vemco Ltd., Shad Bay N.S., Canada). In September 2000, temperature also was logged at about 300 m downstream of the Punt dal Gall dam.

The study sites were accessible only by foot. Access to field sites was constrained in winter by road closures and avalanche danger. From 2000 to 2002, samples were collected at each site one day before and after each flood, and 1 to 2 additional times between the floods during 2000 and 2001. On each visit, we sampled water for chemical analyses and measured turbidity (Nephelometric Turbidity Units (NTU), Cosmos, Züllig AG, Switzerland) and specific conductance (µS cm^{-1}, at 20 °C, WTW LF 340, Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) with portable meters. Water samples were analyzed for ammonium-N, nitrite-N, nitrate-N, dissolved organic and particulate N, soluble reactive phosphorus, total dissolved phosphorus, particulate phosphorus, dissolved organic carbon, and particulate organic carbon following the methods described in Tockner et al. (1997).

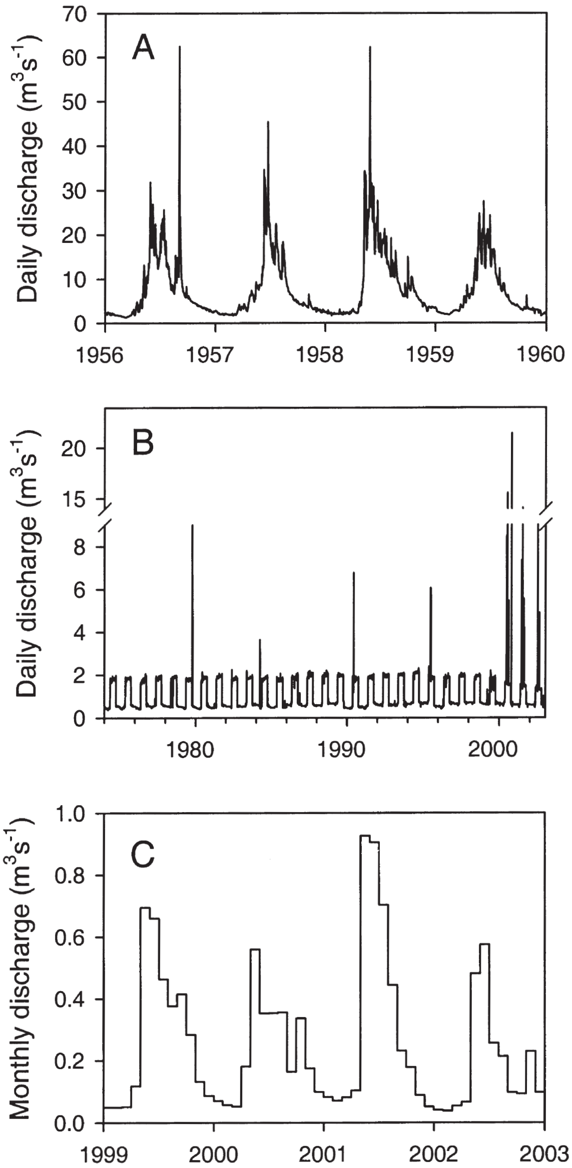

Figure 1. Daily mean discharge in the River Spöl at Punt dal Gall before (A) and after (B) dam completion. Estimated discharge in Val da l'Aqua (C).

Periphyton was assessed by collecting 10 rocks (cobble-size) from each study reach. The rocks were placed in plastic bags, transported to the laboratory in a cooler, and stored at −25 °C until processed (usually within 3 weeks after collection). To remove algae, rocks were scrubbed with a wire brush into a bucket with water, and the dimensions (a, b, c) of each rock were measured with calipers. Aliquots of the algal suspension were filtered through glass fibre filters (Whatman GF/F) for determination of chlorophyll *a* and ash-free dry mass. Chlorophyll *a* was determined by HPLC after extraction with hot ethanol (Meyns et al., 1994). Area values of chlorophyll *a* were calculated for each site as described in Uehlinger (1991). Moss thalli growing on collected rocks were removed with a knife, dried at 60 °C, weighed, ashed at 500 °C for 4 h, and reweighed. Moss biomass, including epiphytic algae, was expressed as g ash-free dry mass m^{-2}.

For diatom analysis, a composite sample from the algal suspensions from the rocks collected on each date was macerated in chromic acid and subsequently washed by centrifugation. Samples were mounted on glass slides with a synthetic resin (Pleurax), and ≥ 250 valves per sample were counted along random transects using a Nikon microscope (Eclipse 600, magnification 400–1000x). Diatom taxa were identified according to Krammer and Lange-Berthalod (1986, 1988, 1991 a, b), Lange-Bertalod and Moser (1994), and Round et al. (1990).

In 2001, we measured sediment respiration in Plexiglas chambers (5.2 cm diameter, 30 cm long) the day before and the day after each flood as changes in O_2 concentration over time. Such measurements also were taken in Val da l'Aqua. At 5 sites within the reach in Val da l'Aqua and 2 reaches (n = 5 per reach) in the Spöl (Punt Periv and site 1.2 km downstream of Punt dal Gall dam), sediment was collected with a shovel after the uppermost sediment layer (ca. 5 cm) had been removed. Sediments were sieved to exclude particles > 8 mm (b-diameter). The chambers were then half filled with the sieved sediment (< 8 mm) and the remaining half with water from the sampling site, sealed with rubber stoppers as described by Jones et al. (1995), and incubated in situ (i.e., chambers were buried at the sampling site) for 6 to 8 h. Oxygen concentration and temperature were measured for each chamber with an oxygen meter (WTW Oxi 340, Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) before sealing the chamber and at the end of the incubation period. After the incubation period, sediments of each chamber were analyzed for particulate organic matter. We determined 2 sediment POM fractions: (1) POM that could be elutriated with water, and (2) POM strongly attached to the sediment grains. The elutriable POM was further divided into the following two size fractions using metal sieves and glass fibre filters (Whatman GF/F): (1) > 1 mm, and (2) 0.7 µm – 1 mm. All POM fractions were determined as ash-free dry mass (i.e., first drying at 60 °C, and then ashing at 500 °C for 4 h).

Between 2000 and 2002, we monitored O_2 concentrations at 30-min to 1 h intervals (WTW Oxi 340) near Punt Periv (2290 m downstream of the dam) for several days before and after floods. For a total of 60 days we used the single station diel O_2 curve to calculate net ecosystem metabolism (Uehlinger and Naegeli, 1998):

$$\beta(t) = \left[K_s (O_2 - O_{2sat}) + \frac{\Delta O_2}{\Delta t} \right] z$$

where $\beta(t)$ is the net O_2 production rate (mg O_2 m^{-2} h^{-1}), $K_s(T,Q)$ is the reaeration rate coefficient (h^{-1}) as a function of temperature T and discharge Q, z is the mean depth (m), $\frac{\Delta O_2}{\Delta t}$ is the change in O_2 concentration between 2 subsequent measurements, and O_{2sat} is the saturation concentration of O_2 (mg O_2 L^{-1}).

Estimates of the reaeration coefficient K_s were based on measurements for the gas exchange of sulfur hexa-fluoride (SF_6) at a discharge of 1.5 $m^3 s^{-1}$ (during summer, the power company kept discharge at 1.5 $m^{-3} s^{-1}$ and tributaries, which could have caused some flow variation, contributed < 2 % to the flow at Punt Periv). A gas mixture of SF_6 and N_2 (1 % v/v SF_6) was injected at a constant flow rate of 1.2 L min^{-1} through 4 fritted glass diffusers. The diffusers were mounted on the stream bed 250 m downstream of the dam. We collected water samples from three stations using 50-mL glass syringes equipped with 3-way valves, leaving no head space; the sampling stations were located 1000, 1510, and 2290 m downstream of the dam. Sampling started about 2.5 h after the beginning of the SF_6 injection at the upstream station (1000 m) and continued to the downstream station (2290 m) within 42 min. The filled syringes were transferred to the laboratory and SF_6 was determined on a gas chromatograph. A detailed description of the sampling procedure and the subsequent analysis is given by Cirpka (1993). We calculated the reaeration coefficient of SF_6 as described by Uehlinger (1998). We multiplied this coefficient by 1.4 to obtain the reaeration coefficient of dissolved oxygen ($K_s(T)$) (O'Connor and Dobbins, 1958) and described the temperature dependence of $K_s(T)$ with an exponential temperature function: $K_s(T) = K_s(20\,°C)\ 1.024^{(T-20)}$ (Elmore and West, 1961). The reach length (x_{crit}), over which the single station method integrated the metabolism ($x_{crit} = v3\,[K_s(T)]^{-1}$, v = current velocity in mh^{-1}), extended between 1650 and 1750 m upstream of Punt Periv.

The average depth was calculated using width, discharge, and the mean travel time of water through the study reach as described by Uehlinger and Naegeli (1998). The mean travel time of water was determined by monitoring the downstream movement of a sodium chloride cloud with conductivity meters. Ecosystem respiration (ER) was calculated as the average net O_2 production rate during the dark period extrapolated to 24 h (respiration rates during the light period were calculated as the average respiration rates of the nights before and after the day of interest). Gross primary production (GPP) was the sum of net O_2 production during the light period and the average dark respiration rate multiplied by the length of the light period.

We used one-way and two-way ANOVA to evaluate the effects of site and/or time on periphyton biomass, sediment organic matter and sediment respiration following data transformation (log (x+1)) to improve normality (Zar, 1984). We applied t-tests to compare periphyton biomass before and after a flood. Finally, we used a principal component analysis (PCA, varimax rotated) to evaluate changes in the community structure of diatoms after arcsin[sqrt(x)] transformation of the relative abundance data of taxa (Zar, 1984). For this analysis, we considered only those taxa with a relative abundance ≥1% (4-year average), i.e., 9 taxa in River Spöl and 6 taxa in Val da l'Aqua. The evaluation of temporal changes in PCA scores was based on one-way ANOVA and linear regression analyses.

Results

Physico-chemical conditions

Following completion of the dam in 1969 until June 2000 when the new flood regime was implemented, flow patterns in the Spöl were highly uniform (Fig. 1B). During this period, flow varied from 1.2 m^3s^{-1} (7 am to 5 pm) to 2.5 m^3s^{-1} (5 pm to 7 am) from May 16 to September 30. During the rest of the year, flow was maintained at 0.5 m^3/s. Significant flows (discharge >3.5 m^3s^{-1}) resulted from high flow releases over the safety gate at the dam crest, and through dam operations such as flushing the safety release gate at the base of the dam or the emptying of Livigno reservoir (Scheurer and Molinari, 2003). Characteristics of the experimental floods and the high flow release of October 2000 are summarized in Table 2. The first flood (June 2000) mainly entrained fine bed sediments, whereas the second flood mobilized substantial amounts of coarse sediments mostly by erosion of lateral debris cones (Mürle et al., 2003). This material was deposited in the channel and on the banks forming point bars and middle bars that then were modified by the subsequent floods. Detailed descriptions of the sediment processes and changes in channel morphology are presented in Mürle et al. (2003). Discharge measured in the Val da l'Aqua reference system varied between 0.08 m^3s^{-1} (30 October 2001) and 0.69 m^3s^{-1} (9 June 1999). The estimated annual flow pattern of Val da l'Aqua is characterized by high flow from May to June/July (mainly snow melt) with a subsequent decline in discharge (Fig. 1C). The hydrograph of the Cluozza River, draining a nearby catchment, indicates that storm induced spates may occur any time between May and November in Val da l'Aqua.

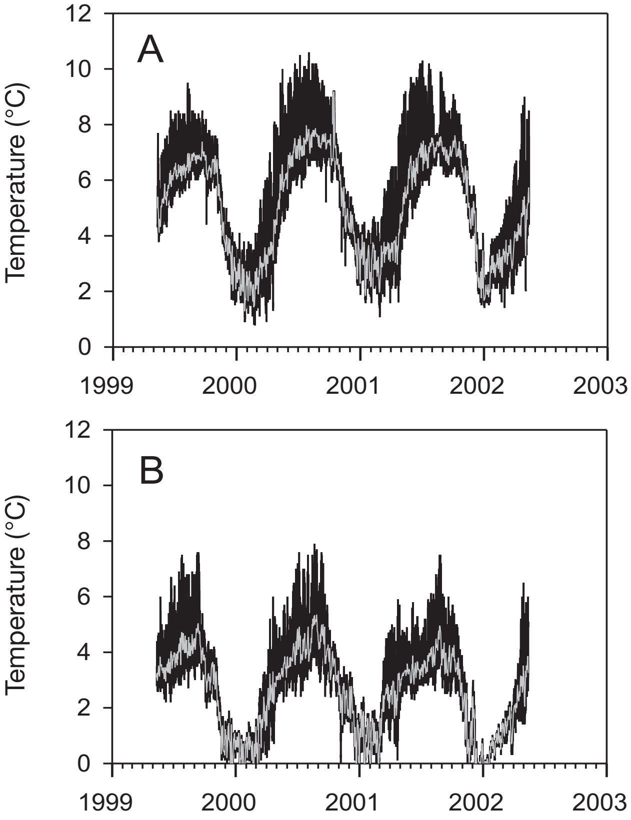

Figure 2. Hourly (black line) and daily mean (gray line) temperatures in the River Spöl at Punt Periv (A) and in Val da l'Aqua (B).

Table 3. Conductivity, turbidity and major nutrients in the River Spöl (Punt Periv) and Val da l'Aqua. Average and standard deviations of spot measurements (n = 36) during base flow conditions.

Parameter	River Spöl	Val da l'Aqua
Conductivity at 20 °C (µS cm^{-1})	248 ± 17	207 ± 44
Turbidity (NTU)	8.3 ± 8.7	9.5 ± 4.5
Soluble reactive phosphorus (µg P L^{-1})	0.8 ± 1.1	0.6 ± 0.7
Total dissolved phosphorus (µg P L^{-1})	2.7 ± 2.3	1.9 ± 1.9
Nitrate (µg N L^{-1})	253 ± 47	247 ± 66

At Punt Periv, temperatures ranged from 5 to 10.5 °C during summer and 1 to 4 °C during winter (Fig. 2). The corresponding temperature ranges in Val da l'Aqua were 2.5 to 8 °C and 0 to 2 °C. Daily mean temperatures were on the average 2.5 °C higher at Punt Periv (Spöl) than in the reference stream. Differences between both sites were greatest in autumn (3.7 – 5.3 °C) and least in spring (0.6 – 0.9 °C). Daily mean temperatures averaged 2.6 °C in January and February at Punt Periv. As a consequence and in contrast to Val da l'Aqua, the Spöl River was not covered by ice and snow in winter.

The turbidity of the River Spöl (Table 3) mainly results from the release of fine particulate matter by a gravel wash facility upstream of the dam. In Val da l'Aqua, turbidity presumably reflects the influence of a small glacier. In the Spöl, deviations of the oxygen concentration from saturation were minor (<1mg O_2 L^{-1}) during periods of enhanced metabolic activity (before floods) because the reaeration was high, i.e., $K_s(T)$ ranged from 2.79 h^{-1} at 6 °C to 3.07 h^{-1} at 10 °C. In the Spöl and Val da l'Aqua nitrate concentrations were relatively high (about 250 µg NO_3-N L^{-1}), reflecting the substantial atmospheric deposition of nitrogen compounds in this part of the Alps (Rhim, 1996). In contrast, average concentrations of soluble reactive phosphorus and total dissolved P were rather low (<1 µg SRP L^{-1}, <3 µg total dissolved P L^{-1}) in both systems.

Moss

Moss (*Fontinalis* spp.) initially was abundant on relatively small rocks (median β-diameter = 62 mm) at Punt Periv. E.g., from May 1999 to June 2000 (before the first flood) about 6 of 10 randomly collected rocks had moss thalli with biomass averaging 137 ± 286 g AFDM m^{-2}. Between the first and third flood about 2 of 10 collected rocks were moss covered, and after the third flood no moss covered rocks were encountered.

Periphyton

Average chlorophyll *a* and ash-free dry mass (AFDM) of periphyton were significantly higher in the River Spöl than in Val da l'Aqua both before and after the implementation of the new flood regime ($p < 0.001$). AFDM paralleled more or less chlorophyll *a*, and the spatial heterogeneity of the periphyton was high (coefficients of variation of chlorophyll *a* and AFDM averaged 91 and 62% in the River Spöl, and 71 and 58% in Val da l'Aqua, respectively). In the River Spöl, all experimental floods coincided with a transient reduction in the average concentration of chlorophyll *a* und AFDM (Fig. 3), although these reductions were not always significant. Differences in post flood recovery resulted in high inter-annual variation in seasonal biomass patterns. In 2000, chlorophyll *a* recovered rapidly after the first flood but not after the second or third flood. The opposite pattern was observed in 2001and 2002. From 2000 to 2002, chlorophyll *a* in the Spöl peaked in autumn and early winter (e.g., 568 mg chlorophyll *a* m^{-2} in October 2001). In Val da l'Aqua, periphyton biomass also tended to increase from late spring to autumn, except in 1999 when biomass peaked in June. Here, rain induced floods occurring at the end of July and beginning of August 2000 coincided with a significant biomass decline.

In the River Spöl, diatoms were associated with thalli of *Hydrurus foetidus*, *Homeothrix janthina,* organic particles and mucilage. Samples also included *Chamaesiphon polonicus*, *Phormidium* sp. *Chantransia* sp. and *Klebsormidium* sp. The list of diatoms collected at Punt Periv comprised 134 taxa, with *Achnanthes biasolettiana* being most dominant (relative abundance 48 ± 17.4%) followed by *Gomphonema angustum* (16.4 ± 16.9%), *Diatoma ehrenbergii* (4.3 ± 5.5%), *Cocconeis placentula* (3.6 ± 3.8%), *Cymbella minuta* (3.4 ± 3.5%), and the *Fragilaria capucina austriaca* group (3.4 ± 7.4%). In Val da l'Aqua, diatoms included 106 taxa. The dominant species was *Achnanthes minutissima* (65.6 ± 18.2%), followed by *Gomphonema angustum* (14.9 ± 11.1%), the *Fragilaria capucina austriaca* group (3.2 ± 5.5%), *Fragilaria arcus* (3.0 ± 3.8%), and *Cymbella minuta* (2.5 ± 3.5%).

After the first flood the relative abundance of *Achnanthes biasolettiana* decreased from >60% to about 20% and *Gomphonema angustum* increased from 9 to 49% in the Spöl. In August 2000, *G. angustum* declined and finally averaged 8.5% between May 2001 and the end of the study in 2002. During this same period, the relative abundance of *A. biasolettiana* varied between 24 and 78% (average 50 ± 15%). The *Fragilaria capucina austriaca* group was relatively rare between 1999 and 2001 (0.6 ± 0.6%) but increased to 16 ± 11% in 2002.

The first three axes of the principal component analysis explained 26, 24 and 18% of the variance, respectively, of the 9 most frequent diatom taxa (average relative abundance ≥ 1%) at Punt Periv. The immediate flood impacts on the diatom community showed no clear pattern (Fig. 4); e.g., distances between two subsequent points in Figure 4 did not differ significantly irrespective of whether the sampling intervals included a flood or not ($p = 0.10$). However, the scores of the first and the third component differed between years ($p < 0.005$) and changed with time between 1999 and 2002 (linear regression, $p < 0.005$). Axis 1 and 2 of the PCA explained 52 and 20% of the variance, respectively, of the 6 most frequent taxa in Val da l'Aqua (data not shown). The scores of axis 2 significantly differed between years ($p < 0.05$) but showed no trend.

The number of taxa found on each sampling date averaged 32 ± 8 (SD) in the Spöl and 18 ± 7 (SD) in Val da l'Aqua, respectively. This difference was highly significant (paired t-test, $p < 0.0001$). Floods usually reduced the number of taxa (except for June and July 2001 in the Spöl); only 4 diatom taxa were found after a major flood in October 2000 in Val da l'Aqua.

Organic matter and sediment metabolism

Total particulate organic matter in the sediments averaged 4.3 and 3.9 g/kg sediment in the River Spöl and Val da l'Aqua, respectively (Table 4). Differences in POM fractions between both systems were not significant except for total POM ($p < 0.05$). Sediment respiration was significantly higher in the Spöl than in Val da l'Aqua (7.6 ± 3.7 vs 1.6 ± 0.5 mg O_2 h^{-1} (kg sediment of grain size

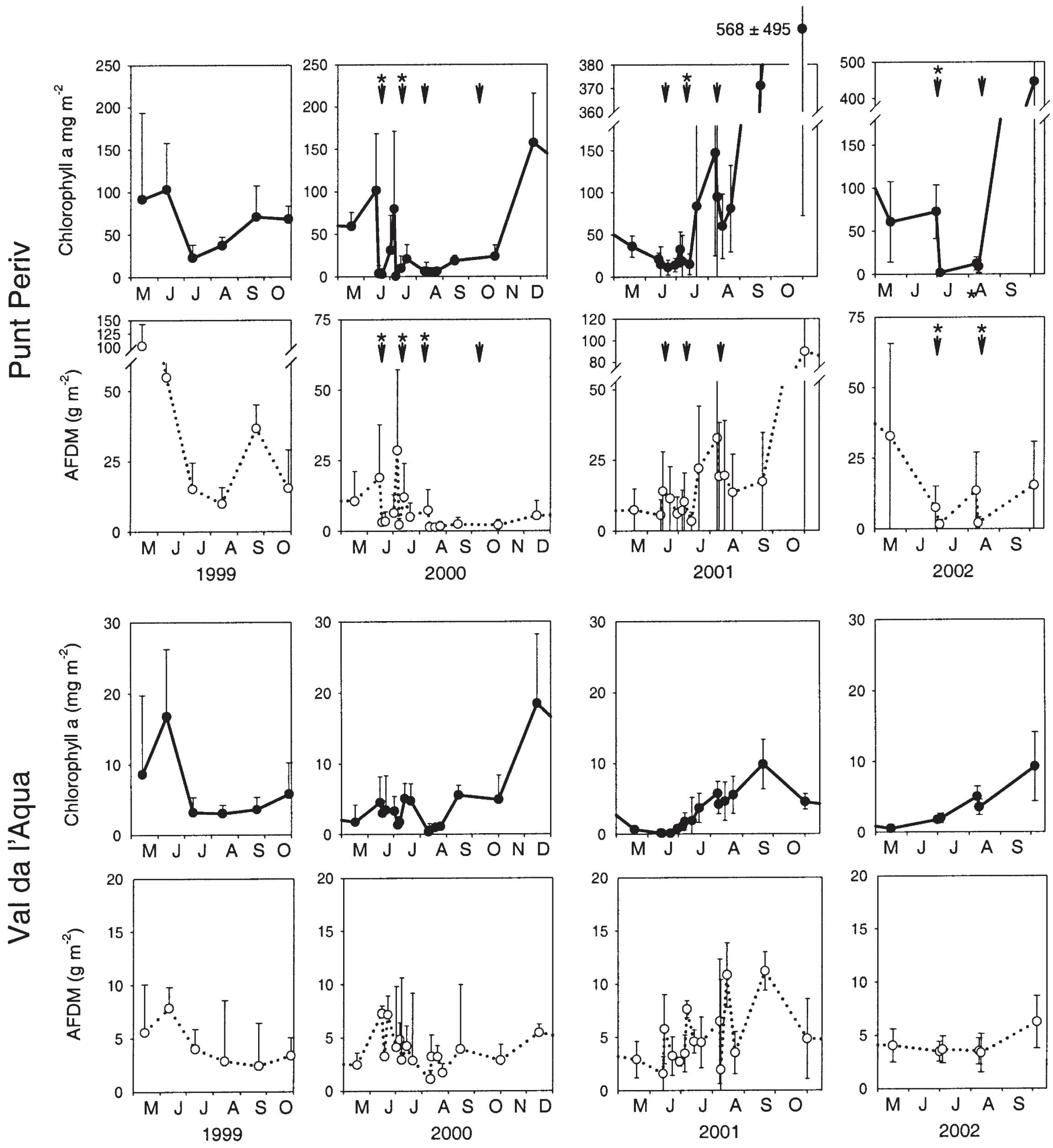

Figure 3. Chlorophyll *a* and ash-free dry mass (AFDM) in the River Spöl (Punt Periv) and Val da l'Aqua. Bars represent ±1 standard deviation and arrows indicate the time of each flood. Floods resulting in significant reductions of chlorophyll *a* and AFDM are marked by an asterisk.

< 8 mm)$^{-1}$, $p < 0.001$). In the River Spöl, where total sediment POM correlated with respiration ($r^2 = 0.33$, $p < 0.001$), the experimental floods did not effect POM levels ($p = 0.31$) but enhanced sediment respiration rates on the average by 62% ($p < 0.0001$).

Ecosystem metabolism

Ecosystem respiration (ER) varied between 0.9 and 5.2 g O_2 m^{-2}d^{-1} (average = 2.5 g O_2 m^{-2}d^{-1}), gross primary production (GPP) between 0.7 and 7.1 O_2 m^{-2}d^{-1} (average = 2.6 g O_2 m^{-2}d^{-1}), and the P/R from 0.2 to 2.4 (average 1.07). The experimental floods reduced gross primary production and ecosystem respiration on average (data of 5 flood events) by 64 and 36%, respectively (Fig. 5 illustrates the impact of the second and third flood in 2001). Because ER was less affected than GPP, P/R declined by 2 to 71% (average 30%). In July 2001, recovery of primary production and ecosystem respiration was relatively fast (Fig. 5).

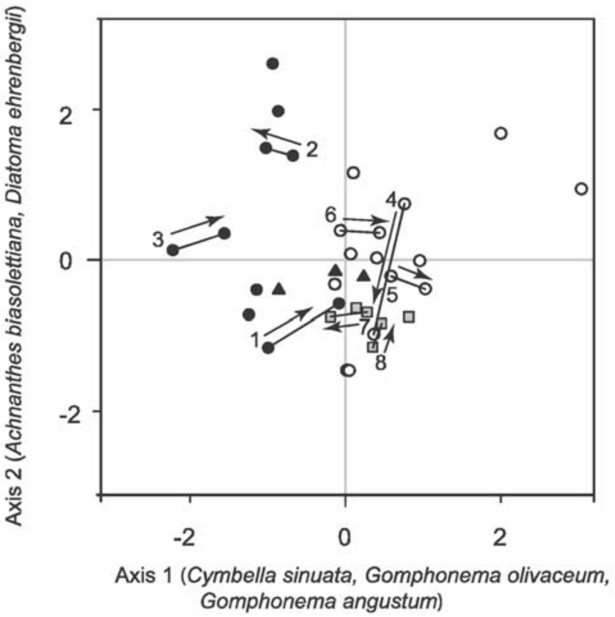

Figure 4. Plot of the principal components results based on the relative abundances of the 9 most frequent diatom taxa in the Spöl River at Punt Periv. Data plotted show diatom communities in 1999 (triangles), 2000 (filled circles), 2001 (open circles), and 2002 (shaded squares). Symbol numbers arranged by flood sequence (e.g., 1 = first flood 2000), solid lines connect before after flood scores and arrows indicate the direction of the flood induced change. Axis labels represent taxa with a factor loading ≥0.7. Axis-1 and axis-2 explained 26% and 24% of the total variance, respectively.

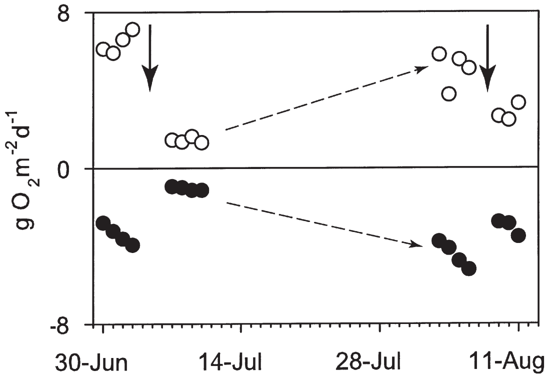

Figure 5. Stream metabolism in the River Spöl upstream of Punt Periv in July and August 2001. Gross primary production (GPP, open circles) and ecosystem respiration (ER, filled circles). Vertical arrows indicate floods (5 July: peak flow = 55 $m^3 s^{-1}$, 7 August: peak flow = 13 $m^3 s^{-1}$). Dashed arrows represent recovery trajectories of GPP and ER.

Table 4. Organic matter content of bed sediments < 8 mm ($\bar{x}$ ± SD, g AFDM kg^{-1}) in the River Spöl and in Val da l'Aqua.

POM fraction	Spöl	Val da l'Aqua
POM total	4.31 ± 0.90	3.98 ± 0.97
POM elutriable >1 mm	0.05 ± 0.09	0.13 ± 0.31
POM elutriable 0.7 µm – 1 mm	0.69 ± 0.57	0.65 ± 0.64

Discussion

The implementation of the flood regime in the River Spöl coincided with changes in ecosystem properties, ecosystem processes, and periphyton community structure. The results showed that floods can result in a temporary biomass reduction, but that the disturbance impact and recovery patterns are not uniform. The outcome is apparently an increased inter-annual variation in seasonal biomass patterns. The floods transiently shifted ecosystem metabolism towards heterotrophy but the metabolism record was too short to indicate possible long-term changes in the energy balance of the system. There are indications of a persistent shift in the structure of the diatom community at the Spöl site since the beginning of the monitoring program.

Periphyton

Before implementation of the new flood regime, periphyton biomass in the River Spöl was about one order of magnitude higher than in Alpine streams with unregulated flow regimes (Table 5). High algal biomass is a common phenomenon below reservoirs or in reaches with regulated flows (e.g., Dufford et al., 1987; Skulberg, 1984; Ward, 1976). Enhanced algal growth is attributed to the lack of spates, and to an increase in nutrient availability and water transparency (Marcus, 1980; Ward and Stanford, 1983). The first three floods resulted in a significant biomass reduction but the biomass even exceeded pre-flood values in the subsequent years (Table 5). Floods apparently enhanced the temporal variation in periphyton biomass. In 2001, the seasonal pattern in periphyton biomass at the two other Spöl sites was similar to those at Punt Periv, although biomass was significantly

Table 5. Periphyton biomass (measured as chlorophyll *a* and ash-free dry mass; $\bar{x}$ ± SD) between mid May and the end of October in the River Spöl (Punt Periv) and a few Alpine streams in the upper Inn River catchment with an unregulated flow regime.

Stream	Altitude m a.s.l.	Chlorophyll *a* (mg chl a m^{-2})	Ash free dry mass (g m^{-2})
Spöl (Punt Periv)	1660		
1999		65.5 ± 30.8	30.5 ± 8.5
2000		25.0 ± 30.7	11.4 ± 12.1
2001		104.5 ± 157.6	28.7 ± 27.2
2002		167.1 ± 191.0	34.4 ± 15.3
Val da l'Aqua[a]	1750	3.9 ± 4.9	4.3 ± 2.2
Fuorn River[b]	1730	4.6 ± 3.7	4.9 ± 3.1
Roseg River[c]	1773	3.3 ± 2.9	2.7 ± 1.5
Güglia[d]	2330	8.3 ± 9.2	4.3 ± 2.6

[a] Average 1999 – 2002, [b] major tributary of the Spöl River (C.T. Robinson & U. Uehlinger, unpublished data), [c] glacier fed river (U. Uehlinger unpublished data), [d] alpine stream (Hieber, 2002).

lower at the uppermost site 0.15 km downstream of the dam (Jakob et al., 2003). The pre-flood monitoring period was relatively short and characterized by longer sampling intervals, which may confound the assessment of the temporal change in biomass. However, the comparison with biomass patterns of Val da l'Aqua also suggests that floods increase biomass variability. In floodprone rivers, the timing and frequency of spates is a major source of variation (Biggs and Close, 1989; Fisher and Grimm, 1988; Tett et al., 1978; Uehlinger et al., 1996). In such systems, periphyton biomass has been shown to recover between spates along trajectories that are linear functions in time (Biggs, 1988; Uehlinger, 1991). After a flood disturbance, abiotic factors such as light, nutrients, and flow are assumed to be major determinants of algal recovery over some time period (abiotic control sensu Fisher and Grimm 1991). If inter-spate periods are short, the abiotic influence prevails and biomass patterns can be explained from discharge patterns (Uehlinger et al., 1996).

In 2000 and 2001, the timing, frequency and magnitude of the Spöl floods were quite similar and both years differed little in respect to flow, nutrient concentrations and temperature. However, seasonal patterns of periphyton biomass were strikingly different, particularly between the relatively short (3–5 weeks) inter-flood periods and a few weeks after the August floods. The immediate flood impacts on the composition of the diatom community were apparently small. However, inter-annual variation was significant with respect to the PCA scores of factors 1 and 3. These PCA scores also showed a significant trend, presumably reflecting the response of the diatom community to the new disturbance regime. In Val da l'Aqua, seasonal differences in periphyton biomass between 2000 and 2001 reflected to some extent the inter-annual variability of the discharge pattern; the minimum in August 2000 may be attributed to floods that occurred after a moderate snow melt fed flow pulse.

The duration of most observational studies on the impact of floods on periphyton and ecosystem metabolism have been limited in time (<2 years, e.g., Biggs and Close, 1989; Fisher et al., 1982; Fisher and Grimm, 1988; Grimm and Fisher, 1989; Uehlinger and Naegeli, 1998). Therefore, we generally lack information on the inter-annual variation in seasonal patterns of biomass and species composition. Moreover, each of the above systems was subject to a particular disturbance regime, which already prevailed for a long time and to which communities became adapted. The apparently unpredictable biomass pattern and the continuous change in the diatom community indicate that the periphyton community of the River Spöl has yet to adapt to the new disturbance regime. This process may require several years and is presumably not linear.

In contrast to periphyton, moss biomass declined after the beginning of the new flood regime. Moss cover on upper stone surfaces declines inversely with the stability of the substratum, which among other factors, also depends on stone size (McAucliffe, 1983). The experimental flood below the Glenn Canyon Dam (Colorado River) showed that bryophytes were more susceptible to high flow than the filamentous macroalga *Cladophora glomerata* (Benenati et al., 2000). The low frequency of high flow events in the Spöl before 1999 favored moss growth also on relatively small rocks, which were highly stable under the residual flows, but were moved or subject to abrasion by moving bed sediment during the experimental floods. These floods were apparently sufficient to eliminate the slow growing moss on small rocks in many riffle habitats. At Punt Periv in the Spöl, moss only remained on some large stable boulders upstream of the study site, and more upstream on coarse gravel at the margins of wide riffles (C.T. Robinson and U. Uehlinger, personal observation). Moss also survived in the uppermost reach because substrata were not affected by moving sediments due to the lack of a sediment source.

Metabolism

An average P/R of >1 indicates that autotrophic energy fixation plays an important role in the metabolism of the canyon-like section of the River Spöl, at least between May and August, but presumably also during the rest of the year. In an incised prealpine river, P/R also exceeded 1 between autumn and spring as long as disturbances were absent for a few weeks (Uehlinger and Naegeli, 1998). The experimental floods shifted the P/R towards heterotrophy because gross primary production was less resistant than ecosystem respiration, a phenomenon already known from other floodprone rivers (Uehlinger, 2000). Similar to these streams, both processes also recovered relatively fast in the Spöl. The extent to which the new flood regime affected annual metabolism rates is unclear because we lack measurements throughout the annual cycle; high biomass during autumn and winter may not necessarily be paralleled by high primary production and ecosystem metabolism (Uehlinger and Naegeli, 1998).

The floods enhanced sediment respiration. Assuming a sediment porosity of 15% and a relative contribution of the sediment fraction <8 mm of 8% to the total sediment volume (U. Mürle, pers. comm.), the flood-induced stimulation of a 0.1 m thick sediment layer would be on average 0.2 g $O_2\,m^{-2}d^{-1}$. Floods may increase sediment POM and, as a consequence, sediment respiration (Naegeli et al., 1995). However, differences between before and after flood concentrations in sediment POM were not significant in the Spöl. In contrast to sediment respiration rates, we observed a decline in ecosystem respiration after each flood, i.e., the results of open system and chamber methods were apparently inconsistent. We hypothesize that the loss of primary producers affects ecosystem respiration by reducing autotrophic respiration. This effect apparently exceeds the stimulation of the hyporheic metabolism. However, the mechanical impact of sampling and presieving sediments may influence the sediment respiration and, thus, impede the comparison of respiration rates obtained from chamber and open-system measurements.

Conclusion

The main reason for the implementation of a flood regime below Punt dal Gall dam was to rehabilitate the rivers potential to maintain channel dynamics and rejuvenate instream habitats. This goal mostly has been met (Mürle et al., 2003). The new flood regime also enhanced the temporal variability in the periphyton community and ecosystem metabolism. The immediate impacts of the experimental floods on benthic primary producers and ecosystem processes were similar to the impact of floods and spates observed in pristine or near natural systems (Fisher and Grimm, 1988; Uehlinger, 2000; Uehlinger et al., 1996). However, a few short floods per year cannot restore the lost dynamics of an Alpine mountain river where the snow or ice melt driven flow pulse results in a characteristic seasonal periphyton pattern – low biomass during summer and high biomass in autumn (Kawecka, 1980; Uehlinger et al., 1998). After 3 years of artificial floods, periphyton patterns resembled more those of a flood prone prealpine river than of an Alpine mountain river. However, this period is presumably too short to determine the long-term effects of such experimental floods.

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