RIVER RESEARCH AND APPLICATIONS

River Res. Applic. 20: 359-377 (2004)

Published online 10 February 2004 in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/rra.743

STREAM ECOSYSTEM RESPONSE TO MULTIPLE EXPERIMENTAL FLOODS FROM A RESERVOIR

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ABSTRACT

The effects of multiple experimental floods in the same year on the ecology of a river (River Spöl) below a large reservoir were investigated. In the flood year (2000), three floods of different magnitude (10 m³/s on 15 June, 25 m³/s on 5 July, and 10 m³/s on 10 August) were implemented, each lasting 7-8 h. Regulated baseflow discharge was maintained at less than 2.5 m³/s. Samples of macroinvertebrates, periphyton, water chemistry, and seston were collected for one year (1999) before and then immediately before and after each flood in the Spöl and in an adjacent reference tributary (Val da l'Aqua). Samples also were collected periodically between floods to evaluate temporal response patterns. During two of the floods, suspended sediments and seston were measured at 30 min to 1 h intervals. Suspended sediment and seston reached peak concentrations within the first hour of each flood, then decreased within about 2 h. Peak seston and suspended sediment concentrations during each flood decreased by an order of magnitude from the July flood to the August flood. Two-way ANOVA indicated significant flood effects on periphyton standing crops expressed as either chlorophyll a or ash-free dry mass (AFDM). Recovery of periphyton following each flood appeared to be progressively slower after the later (July and August) floods. Seston chlorophyll levels also were lower following each flood, being significantly correlated to periphyton biomass. Two-way ANOVA indicated that the floods significantly decreased macroinvertebrate taxonomic richness, density, and biomass. Taxa that decreased from the floods included the turbellarian Crenobia alpina and the gammarid Gammarus fossarum. Taxa that showed a fast recovery to the floods included the Chironomidae, Simuliidae, and Baetidae. Our data indicate a strong temporal effect of flood disturbance on benthic assemblages (periphyton and macroinvertebrates) below reservoirs that partly reflects species-specific life histories and traits, and the cumulative effects of earlier floods. Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS: Switzerland; periphyton; flow regime; Gammarus; Fontinalis; temporal

INTRODUCTION

Large dams are prominent features of most rivers (Ward and Stanford, 1983; Pringle, 2001; Stanford and Ward, 2001). Indeed, there are around 40 000 large dams (>15 m high) worldwide (Oud and Muir, 1997; Jackson *et al.*, 2001). Reservoirs behind large dams are used for power production, irrigation, navigation, water supply, recreation, and flood control. Recently, ecological purposes for large dams also have been mandated (Marzolf *et al.*, 2000). Large dams in the Alps are used strictly for power production with streams below these dams having greatly reduced flows or even absence of instream flow due to abstraction/diversion of the water to power plants several kilometres downstream. River reaches downstream of dams become physically and biologically altered because of major changes in geomorphological controls (Ward and Stanford, 1979; Gore and Petts, 1989; Wallace, 1990; Ligon *et al.*, 1995; Patten *et al.*, 2001) and changes in longitudinal and lateral exchange processes (Ward and Stanford, 1983, 1995; Ward, 1989). Two primary physical effects of dams on downstream receiving waters are alterations of natural temperature and flow regimes. Typically, temperatures become more constant (see Vinson, 2001), flows often reduced, and flow regimes deviate from natural conditions (Poff *et al.*, 1997; Vinson, 2001). Lateral linkages within the land–water interface also are constrained by the loss of the flood pulse so important for sustaining riverine structure and function (Junk *et al.*, 1989; Benke *et al.*, 2000).

Instream biotic assemblages also shift in response to the altered habitat templet resulting from changes in environmental conditions (sensu Southwood, 1988), usually showing orders-of-magnitude increases in abundances and

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standing crops (Vinson, 2001) and assemblages made up of organisms adapted to more constant or stable environments (Armitage, 1976; Poff and Allan, 1995). For instance, changes in the flow regime can have important ramifications on the growth and development of instream algae and macrophytes and the maintenance of riparian vegetation (Stromberg and Patten, 1990; Müller, 1995; Molles *et al.*, 1998). As such, there has been much recent attention towards the importance of restoring the natural flow regime to regulated rivers in hopes of enhancing their ecological integrity (Sparks, 1995; Petts, 1996; Poff *et al.*, 1997; Galant *et al.*, 1998; Sparks *et al.*, 1998; Dudgeon, 2000; Pringle *et al.*, 2000) or by the removal or breaching of dams (Pringle, 2001; Hart *et al.*, 2002).

The breaching of smaller dams has become increasingly common (Poff and Hart, 2002), especially in North America where many dams are outdated and in need of renovation (Hart et al., 2002). For instance, around 180 dams have been removed in the USA in the last decade (Born et al., 1998; Jackson et al., 2001). However, many dams, large dams in particular, will remain in place for purposes of hydropower, flood protection and other waterregulating measures, with around 260 new large dams becoming operational each year (McCully, 1996). Thus, remedial measures other than removal are needed to improve habitat conditions of rivers below these dams (Kondolf and Wilcock, 1996). The implementation of such measures is usually complex because of water ownership, water allocation, and the multiple interest groups involved in management decisions (see Andrews and Pizzi, 2000; Patten et al., 2001). For example, the single experimental flood below Glen Caynon Dam was preceded by research studies begun 13 years before the actual flood was conducted (Webb et al., 1999). The research programme for the flood itself required two years of planning (Patten et al., 2001). Andrews and Pizzi (2000) list a number of legal, economic and physical constraints on the Glen Canyon test flood and their subsequent resolutions. These complexities for implementing restoration measures to downstream receiving waters probably vary considerably among dams and, of course, the specific restoration measure. Partial restoration of the natural flow regime, e.g. by experimental flooding, can be economically costly (Andrews and Pizzi, 2000) but ecologically the most beneficial (Poff et al., 1997).

Our study was conducted on the River Spöl below a large dam (Punt da Gall) situated on the border between Switzerland and Italy. Below the dam, the Spöl flows in a confined channel through the Swiss National Park. Operation of the dam since 1970 has resulted in constant residual flows of less than 2.5 m^3 /s (see below), with concomitant effects on riverine habitats (channel morphology) and biota (after Ward and Stanford, 1979). For example, reduced flows have favoured the clogging of the streambed by fine sediments and allowed the formation of side-slope debris fans into the main channel (the primary source of coarse sediments), causing the development of pools upstream. An agreement was made between Park authorities and the power company to use artificial flooding to restore habitat conditions and improve the fishery in the river downstream of the dam. The agreement consisted of implementing three experimental floods during the summer (June, July and August; see below) of each year over a period of three years (Scheurer, 2000). Although a number of studies have examined the effects of single floods (flushing flows) on riverine ecosystems (Reiser et al., 1985; Kondolf and Wilcock, 1996; Molles et al., 1998; Patten et al., 2001), we are aware of only one other study that examined the effects of multiple experimental flows within the same year (Williams and Winget, 1979). In this report we evaluate the response of benthic communities (periphyton and macrozoobenthos) to the floods in 2000 relative to the previous year of regulated flow; essentially a before-after-control-impact (BACI) design (Underwood, 1992). Our primary objectives were to assess (1) the cumulative effects of the floods in relation to their timing within the year, and (2) any differential effects from floods of different magnitude.

METHODS

Description of study sites

The study was conducted in the Swiss National Park on the River Spöl flowing from the Livigno Reservoir in Italy (Figure 1); the reservoir dam (Punt da Gall) sits on the border between the two countries. The river below the dam flows through a confined canyon and the study reach (Punt Periv) is situated about 2.3 km downstream of the dam (coordinates: $10^{\circ}11'$ N, $46^{\circ}38'$ E). The maximum elevation of the Spöl catchment is 3302 m a.s.l. and 1660 m a.s.l. at the study site (Table I). Although the entire catchment area of the Spöl is 286 km^2 (1% glaciated), the catchment area downstream of the dam is only 6 km^2 . Stream width of the study reach ranged from 10 to 18 m,



Figure 1. Map of the study region in Switzerland. The open circles indicate the locations of the study reaches on the Spöl (Punt Periv) and the adjacent tributary (Val da l'Aqua). Val da l'Aqua was used as the reference site for comparison with results from the River Spöl. The dam is on the border of Switzerland and Italy

Table I.	Physical a	and chemical	characteristics	of the	study	sites	based	on spot	measures	recorded	on	each	visit	during	1999
(n = 6) a	and 2000 (<i>i</i>	n = 15)													

	Spö	öl	Val da l'Aqua		
Parameter	Mean	SD	Mean	SD	
Catchment area at study site (km ²)	286		4.3		
Catchment area between dam and study site (km ²)	6				
Percentage catchment glaciated	1		0.2		
Elevation at study site (m a.s.l.)	1660		1750		
Channel slope range (%)	1-2		5-6		
Channel width range (m)	10-18		3–7		
Temperature (°C)	7.7	1.3	4.4	0.9	
Conductivity (µS/cm)	248	16	197	35	
Turbidity (NTU)	10.2	9.9	11.2	4.3	
Nitrate-N (NO ₂ +NO ₃ , μ g/l)	271	55	255	62	
Particulate nitrogen (PN, µg/l)	21.6	10.8	8.7	9.6	
Phosphorus (SRP, µg/l)	0.87	1.20	0.48	0.60	
Particulate phosphorus (PP, µg/l)	6.0	4.0	3.1	1.8	
Silicate oxide (SiO ₂ , μ g/l)	2.3	0.7	1.4	0.5	
Dissolved organic carbon (DOC, µg/l)	0.86	0.46	0.60	0.32	

with a slope of 1–2%. Stream substrata consisted of alluvial cobbles and boulders with some bedrock outcrops also present. Following dam construction, the residual flow in the Spöl was 1.5 m³/s at night and 2.5 m³/s during the day. After September 1999 discharge in the Spöl was reduced to 0.70 m^3 /s until 16 May 2000 when summer base-flow was maintained at 1.6 m^3 /s.

A reference stream (Val da l'Aqua) was selected that flows into the River Spöl about 0.8 km downstream of the Spöl study reach (Figure 1). Although this system contrasts physically with the Spöl, it represents a nearby stream with a natural flow regime and biota adapted to this natural stream environment. Data from this site were used to examine unregulated temporal patterns over an annual cycle in periphyton and macroinvertebrate abundances. Val da l'Aqua drains a 4.3 km² catchment with a small block glacier (representing 0.2% of the catchment area) near its headwaters (Table I). Its catchment has a maximum elevation of 3126 m a.s.l. and the study site was at 1750 m a.s.l. The gradient of the 150 m long study reach was around 5–6%. Stream width ranged from 3 to 7 m, and substrata were mostly alluvial sediments of cobbles and boulders. Discharge in Val da l'Aqua averaged 0.38 m³/s (range 0.06–0.69 m³/s; coefficient of variation, CV = 59%) based on periodic discharge measurements (usually monthly) completed on site (n = 8) from October 1999 to December 2000. Primary water sources are groundwater, snow melt in spring, and melt water from the block glacier.

The experimental floods

Figure 2 shows the discharge regime of the River Spöl for three typical years (1960–1962) before dam construction (full operation in 1974), a typical year after dam construction (1999 in the figure), and the regime during 2000 indicating the three experimental floods along with a high flow release in October 2000 caused by heavy precipitation that filled the reservoir above capacity. The reduction in residual flows following September 1999 provided enough water for the floods to be a cost-neutral experiment. The experimental flood peaks (m³/s) were comparable to those before dam construction, but the average daily flows during each flood were lower than pre-dam values because flood durations were less. Flow peaks of each flood were 16 m³/s with a discharge of 10 m³/s for about 7.5 h on 15 June 2000, peak flow of 43 m³/s and discharge of at least 25 m³/s for about 7.5 h on 5 July 2000, and a peak flow of 12 m³/s with a discharge of 10 m³/s for about 7 h on 10 August 2000. The peak flow in October reached 30 m³/s and extended over three days with an average daily discharge of 20 m³/s. The rising and receding limb of each flood was physically constrained by the flow release mechanism of the dam, i.e. engineering constraints of the flow control gates. Normal and flood releases were hypolimnetic, thus we expected little change in temperature or chemistry during the floods.



Figure 2. Typical flow regime of the River Spöl before dam construction (years 1960 to 1962), after dam construction (1999), and during the experimental flood year (2000). The dam was constructed in 1970 and became operational in 1974. The flow in 1999 represents the residual flow maintained below the dam with all excess water being diverted through pipes for power production lower in the basin. The numbers above the flow peaks in 2000 are the average daily flows (in m³/s)

Field measures recorded during the floods

During the 5 July and 10 August floods, conductivity (WTW model LF340, Weinheim, Germany) and water temperature were recorded, and a 11 water sample was collected at predetermined time intervals and analysed for total suspended sediments and ash-free dry mass (AFDM). In addition, a seston sample (n = 4, 100 µm mesh) was collected at the same time as suspended sediments and analysed for chlorophyll *a* and *b*, and AFDM as described below. Chlorophyll *a* was used as a measure of total algal biomass, whereas chlorophyll *b* was used for estimates of filamentous macro-algae. We also collected water samples hourly during the 5 July flood for analysis of nitrogen constituents (ammonium and nitrate-N) and soluble reactive phosphorus.

General field protocols

Field sampling began about one year prior (mid-May 1999) to the experimental flooding. Samples were collected from each 100 m long study reach on five separate visits in 1999 (four to five week intervals) with the final collection made in November 1999, except for periphyton (see below) which was collected on six dates in 1999. Study reaches could only be reached by foot and thus were selected for accessibility (e.g. upstream of trail crossings), although reaches were representative of general stream conditions. Access to field sites was closed during winter 1999 due to road closures and avalanche danger; sample collection resumed in May 2000. During 2000, samples were collected the day before each flood, the day after each flood, and at periodic intervals (usually two additional times) between each flood. Fifteen separate visits were made to the field sites in 2000, the last collection on 14 December. Temperature loggers (Vemco Inc., Nova Scotia, Canada) were installed at each site on the first visit and periodically downloaded over the two-year study. Discharge for the River Spöl was recorded by the Swiss Hydrologic and Geologic Survey. Discharge was periodically measured at Val da l'Aqua using a salt dilution method (Gordon *et al.*, 1992).

On each visit at each site we collected benthic macroinvertebrates (n = 3), drift and seston (n = 4), periphyton (n = 10), and 11 water samples for chemistry. Benthic macroinvertebrates were collected from riffle/run habitats using a modified Hess sampler $(0.01 \text{ m}^2, 100 \text{ µm} \text{ mesh})$ and preserved in the field with 70% ethanol. Drift/seston was collected during the day using a nitex net (length 1 m, aperture 11 cm, 100 µm mesh) for a period of 1 to 3 min each depending on net clogging. Velocity was measured at the mouth of the net using a MiniAir II velocity meter (Schiltknecht AG, Zürich, Switzerland) for estimating the volume of water filtered. These samples were returned to the laboratory in plastic storage bags and frozen at -25° C until processed. Periphyton was assessed by collecting ten random rocks (cobble-sized) from each reach on each date, placing the rocks in a plastic storage bag, and keeping them frozen at -25° C until processed in the laboratory (usually within three weeks of each collection). Turbidity (nephelometric turbidity units, NTU; Cosmos, Züllig AG, Switzerland) and conductivity were measured in the field on each sample date. The 11 water sample collected on each date was returned to the laboratory and filtered for analyses of ammonium, nitrite-N, nitrate-N, dissolved and particulate N, soluble reactive phosphorus, dissolved organic carbon, and particulate organic carbon following methods in Tockner *et al.* (1997). Silicate (SiO₂) concentrations also were determined on some dates (n = 6).

In the laboratory, benthic macroinvertebrates were hand-picked from each sample using a dissecting microscope at $10 \times$ magnification, identified to lowest practical taxonomic unit (usually genus), counted, dried at 60°C and weighed for biomass estimates. The remaining material from each benthic sample was then dried at 60°C, weighed, burned at 550°C, and reweighed for estimates of benthic organic matter (BOM) as AFDM. Drift/seston samples were filtered through Whatman GF/F glass microfibre filters. First, the number and identity of macroinvertebrates were determined from each sample. Next, the filter was cut in half. One half was used for chlorophyll *a* and *b* analysis, and the other half for determination of AFDM following methods in Uehlinger (1991). Briefly, chlorophyll was extracted by boiling for 10 min in 90% ethanol and chlorophyll *a* and *b* measured by high performance liquid chromatography (HPLC) (Meyns *et al.*, 1995). Large invertebrates were removed from each filter prior to determination of seston biomass.

Periphyton biomass was estimated for each rock. When present, moss was removed from the rock before being assessed for periphyton. Moss biomass was measured as AFDM. Periphyton was removed from each rock using a metal bristle brush and rinsing. Aliquots of this slurry were filtered through two Whatman GF/F filters. One filter was used for analysis of chlorophyll *a* and *b*, and the other for periphyton AFDM. Periphyton biomass was

expressed as grams per square metre (g/m²) following Robinson *et al.* (2000). Most benthic parameters were analysed using two-way ANOVA (site and time as effects) following data transformation $(\log(x + 1))$ to improve normality (Zar, 1984).

RESULTS

General physico-chemical characteristics

Table I lists the mean values of nine parameters measured at each site on each visit. In general, the Spöl was warmer $(7.7^{\circ}C)$ than Val da l'Aqua (4.4°C). The Spöl also showed higher although comparable values than Val da l'Aqua in other measured constituents (e.g. conductivity, phosphorus and nitrogen). Nitrate nitrogen showed values typical of most streams and rivers in the Alps (e.g. Malard *et al.*, 2000). Silicon, measured as silicate oxide, was above limitation levels for diatom growth at both sites.

Physico-chemical conditions during the floods

Little chemical response was observed during the 5 July flood. Only nitrate-N increased with increasing discharge (from 290 to 330 µg/l). Ammonium-N showed irregular fluctuations (mean 7.7 µg/l, SD 4.5 µg/l), whereas concentrations of nitrite-N ($0.9 \pm 0.5 \mu$ g/l) and soluble reactive phosphorus (SRP, $1.5 \pm 0.9 \mu$ g/l) essentially did not change during flooding. Conductivity and temperature, recorded continuously during the 5 July and 10 August floods, also showed no change in values (conductivity 228 ± 9 and 226 ± 9 µs/cm, respectively; temperature 6.7 ± 0.2 and 7.1 ± 0.4°C, respectively).

Suspended sediment concentration increased with the increase in discharge, peaking within the initial 1.5 h of flooding on both 5 July and 10 August (Figure 3). Peak values of suspended sediment during the 5 July flood $(25 \text{ m}^3/\text{s})$ were over 20 times greater than those in the 10 August flood $(10 \text{ m}^3/\text{s})$. Peak values typically decreased following the initial hour of each experimental flood, but remained slightly elevated for the remaining flood period, especially during the 5 July flood. These data indicate that most of the transport of fine sediments occurred during the initial period of flooding.

Seston (>100 μ m), as chlorophyll *a* and *b*, and AFDM, increased to peak concentrations during the initial hour of flooding then decreased after about 2 h (Figure 4). Changes in seston concentration provided an indication of the degree of algal scouring taking place during each flood. Pre-flood baseflow concentrations were less than 2 mg/m³ chlorophyll *a*, less than 0.50 mg/m³ chlorophyll *b*, and less than 20 mg/m³ AFDM. Chlorophyll concentrations reached over 250 mg/m³ chlorophyll *a* and 90 mg/m³ chlorophyll b in the July flood, being 2.5–3 times greater than those in the August flood. The amount of total organic matter (as AFDM) peaked at about 130 g/m³ in the July flood, three times higher than the peak amount measured in the August flood.

Flood effects on stream benthos

Benthic organic matter and periphyton. The overall amount of BOM was similar between the Spöl and Val da l'Aqua, ranging from around 5 to 25 g AFDM/m² (Figure 5). BOM tended to peak during summer in 1999, especially in the Spöl, although a reduction in BOM was observed in Val da l'Aqua in August. There was a substantial decrease in BOM levels in the Spöl after the large flood in July that was not as clearly evident in post-flood samples from the smaller floods in June and August. However, BOM levels recovered to pre-flood concentrations rapidly after each flood; this pattern again was most clear following the large flood in July.

Two-way ANOVA indicated significant flood effects on periphyton biomass, expressed as either chlorophyll *a* (interaction term, $F_{1,20} = 21.73$, p < 0.0001) or AFDM (interaction term, $F_{1,20} = 13.64$, p < 0.0001) (Table II, Figure 5). Chlorophyll *b* data showed similar patterns to chlorophyll *a* and thus are not shown. Recovery of periphyton biomass in the Spöl occurred rapidly following the first flood, attaining levels measured prior to the flood. However, periphyton biomass remained relatively low and at similar levels to those in Val da l'Aqua after the July flood. Periphyton biomass was always low in Val da l'Aqua and varied little among dates. The periphyton decrease in September 1999 in Val da l'Aqua was in response to high flows from a rainstorm, a response not observed in the flow-regulated Spöl (Figure 5). Chlorophyll concentrations increased dramatically in the Spöl in December 2000



Figure 3. Total and organic (as AFDM) suspended sediment concentrations (g/m³) in the river water during the floods of 5 July and 10 August 2000

due to a proliferation of the filamentous algae *Hydrurus foetidus* (authors, personal observation), a common algae of alpine streams in winter.

Seston biomass. Seston concentrations in 1999 typically were higher in the Spöl than in Val da l'Aqua (Table II), primarily due to the higher algal levels (as chlorophyll *a*) in the seston in the Spöl (Figure 6). Val da l'Aqua experienced a major peak in seston AFDM in September 1999 during a heavy rainstorm that increased discharge to flood levels. This rain event was not noticeable in the regulated discharge of the Spöl, although sestonic chlorophyll *a* levels increased by about two to three times on this date relative to the other sample dates in 1999. Seston levels tended to be lower in the periods between floods, likely reflecting the reduced periphyton biomass at these times (the correlation of periphyton chlorophyll to seston chlorophyll in 2000 was significant; r = 0.91, p < 0.05).

Macroinvertebrate assemblages. Two-way ANOVA indicated that the floods had a significant impact on the richness (interaction term, $F_{1,19} = 2.94$, p = 0.0003), density (interaction term, $F_{1,19} = 3.99$, p < 0.0001) and biomass (interaction term, $F_{1,19} = 3.98$, p < 0.0001) of macroinvertebrates in the River Spöl (Table III, Figure 7). In Val da l'Aqua, these parameters showed relatively little change over the two-year period of study, i.e. average taxonomic richness ranged from six to nine taxa, density was typically less than 5000 individuals (ind.)/m², and biomass was less than 5 g/m². In the Spöl, average taxon richness was 11 in 1999 and decreased to 7.4 taxa following the first flood on 15 June 2000, staying at less than nine taxa for the remainder of the study.

The mean pre-flood density in the Spöl in 1999 was 19 300 ind./m², whereas it averaged 9525 ind./m² in 2000. The overall density decrease in 2000 mostly was caused by the 5 July flood that reduced density to around



Figure 4. Seston concentrations (>100 μ m, mg/m³) as chlorophyll *a* and *b*, and AFDM in the river water during the floods of 5 July and 10 August 2000: *n* = 3 as mean ±1 SD. All symbols have error bars but they may be shorter than the size of the symbol

1000 ind./m² (Figure 7). The first flood had no significant effect on density (mean comparison of 13 June and 16 June, Tukeys test, p > 0.05), although the high variance in density (coefficient of variation = 148%) following this flood suggests the effect was patchy. The increase in macroinvertebrate density prior to the second flood was due to an influx of chironomids (see below). Densities also decreased from the August flood, from 12 220 before to 3860 ind./m² after the flood. Presumably the flood in October also decreased densities, although sampling occurred about a week after the flood. Macroinvertebrate density increased in December 2000 to values observed before the floods, but the assemblage composition was quite different (see below).

The floods reduced macroinvertebrate biomass in the Spöl from an average 12.3 g/m^2 in 1999 to 3.4 g/m^2 in 2000 (Table III, Figure 7). Biomass was not affected initially by the first flood, but decreased over time following this flood. The July flood decreased biomass from 1.7 g/m^2 before the flood to less than 0.4 g/m^2 the day after the flood. Biomass increased to around 4 g/m^2 before the August flood, decreasing then to around 1.7 g/m^2 . The flood in October also reduced the biomass of macroinvertebrates in the Spöl; biomass was less than 0.2 g/m^2 in the week following this flood. Average biomass then increased to 2.6 g/m^2 in December 2000.



Figure 5. Mean (± 1 SD) benthic organic matter (BOM, g/m², n = 3) associated with benthic Hess samples, and periphyton standing crops (mg/m², n = 10 stones) as chlorophyll *a* and AFDM. Arrows indicate the time of each flood during 2000

Table II. Results of two-way ANOVA testing for effects of flooding on benthic organic matter, periphyton standing crops as chlorophyll *a* and ash-free dry mass, and seston biomass as chlorophyll *a* and ash-free dry mass

Variable	Effect	df	<i>F</i> -value	<i>p</i> -value
Benthic organic matter	Site	1	2.77	0.099
U	Date	19	2.34	0.0036
	Site-Date	19	0.76	0.752
Periphyton chlorophyll a	Site	1	440.69	< 0.0001
	Date	20	45.12	< 0.0001
	Site-Date	20	21.73	< 0.0001
Periphyton AFDM	Site	1	308.41	< 0.0001
1 5	Date	20	19.74	< 0.0001
	Site-Date	20	13.64	< 0.0001
Seston chlorophyll a	Site	1	217.83	< 0.0001
1 5	Date	17	44.12	< 0.0001
	Site-Date	17	15.98	< 0.0001
Seston AFDM	Site	1	2.28	0.132
	Date	17	36.69	< 0.0001
	Site-Date	17	13.07	< 0.0001



Figure 6. Mean (± 1 SD) seston concentrations (n = 4, mg/m³) as chlorophyll a and AFDM. Arrows indicate the time when each flood occurred in 2000. The large peak in concentration in September 1999 was from samples collected during a major rain-runoff event

Variable	Effect	df	<i>F</i> -value	<i>p</i> -value	
Taxon richness	Site	1	31.27	< 0.0001	
	Date	19	3.25	< 0.0001	
	Site-Date	19	2.94	0.0003	
Density	Site	1	56.93	< 0.0001	
2	Date	19	4.26	< 0.0001	
	Site-Date	19	3.99	< 0.0001	
Biomass	Site	1	87.18	< 0.0001	
	Date	19	3.75	< 0.0001	
	Site-Date	19	3.98	< 0.0001	

Table III. Results of two-way ANOVA testing for effects of flooding on macroinvertebrate taxon richness, density and biomass. Values were log(x + 1) transformed prior to analysis

Macroinvertebrate taxa response. There were clear taxon-specific responses to the floods. Figure 8 shows the density response for eight abundant taxa with the results of the two-way ANOVA for each taxon presented in Table IV. Taxa that clearly decreased as a result of the floods included the turbellarian *Crenobia alpina* and the gammarid *Gammarus fossarum*. Turbellarian numbers decreased after the first flood and never really recovered in 2000. They were also low in abundance in Val da l'Aqua. *Gammarus fossarum* density decreased after each flood, although they recovered to pre-flood levels before the July flood. Following the July flood, gammarid



Figure 7. Mean (± 1 SD) macroinvertebrate taxon richness (taxa/m²), density (no./m²) and biomass (g/m²) from benthic Hess samples (n = 3) collected on each sample date. All symbols have error bars but they may be shorter than the size of the symbol. Arrows indicate the time that each flood occurred in 2000

numbers remained at less than about 5000 ind./m². Gammarid density began to recover in autumn following the August flood but was again reduced in October and showed no increase by December 2000. Gammarids were never collected in Val da l'Aqua. Trichopterans (mostly Limnephilidae and Rhyacophilidae) also attained rather high densities (c. 2400 ind./m²) at certain times before the flood year, but densities were always low (< 100 ind./m²) in 2000. Trichopteran densities also were low in Val da l'Aqua (Figure 8).

Taxa that showed fast recovery responses to the floods included the Chironomidae, Simuliidae and Baetidae (*Baetis alpinus* and *Baetis rhodani*) (Figure 8). The Chironomidae increased to high densities following the first flood (>16 000 ind./m²), although the major flood in July caused a substantial decrease in chironomid numbers with no appreciable increase in numbers evident until December 2000. Simuliid numbers increased dramatically before the major flood in July (c. 7000 ind./m²), again before the August flood, and again in autumn. The Baetidae also demonstrated high resistance to the floods. Baetid densities always decreased after each flood, but recovery to pre-flood densities was evident prior to the next flood and numbers in December 2000 were similar or higher to those in 1999.



Figure 8. Mean density $(no./m^2)$ of common macroinvertebrate taxa collected in the benthic Hess samples (n = 3) at each site and date. Arrows indicate the time that each flood occurred in 2000. Errors bars are not shown in order to better illustrate temporal patterns in abundance

Two taxa showed disparate responses to those mentioned above. The Heptageniidae were low in abundance in the River Spöl in 1999 and numbers remained low in 2000 (Figure 8). The Heptageniidae (*Rhithrogena* sp.) were a predominant taxon in Val da l'Aqua, as were the Plecoptera (mostly Nemouridae) and Baetidae (namely *Baetis alpinus*). Plecoptera abundance was reduced from the June flood from an average 1400 to 120 ind./m², and from 340 to <40 ind./m² from the July flood. However, plecopteran density increased to over 13 000 ind./m² by December 2000, even surpassing values observed in 1999.

Variable	Effect	df	<i>F</i> -value	<i>p</i> -value
Plecoptera	Site	1	135.16	< 0.0001
1	Date	19	6.27	< 0.0001
	Site-Date	19	4.21	< 0.0001
Chironomidae	Site	1	28.56	< 0.0001
	Date	19	3.31	< 0.0001
	Site-Date	19	3.62	< 0.0001
Baetidae	Site	1	1.77	0.186
	Date	19	2.34	0.0038
	Site-Date	19	1.58	0.075
Trichoptera	Site	1	172.09	< 0.0001
	Date	19	6.65	< 0.0001
	Site-Date	19	5.09	< 0.0001
Turbellaria	Site	1	114.91	< 0.0001
	Date	19	5.13	< 0.0001
	Site-Date	19	3.04	0.0002
Gammaridae	Site	1	788.26	< 0.0001
	Date	19	2.63	0.0011
	Site-Date	19	2.49	0.0019
Heptageniidae	Site	1	396.94	< 0.0001
	Date	19	5.05	< 0.0001
	Site-Date	19	4.11	< 0.0001
Simuliidae	Site	1	40.73	< 0.0001
	Date	19	2.94	0.0003
	Site-Date	19	2.24	0.0057

Table IV. Results of two-way ANOVA testing for the effects of flooding on selected common macroinvertebrate groups. Density values were transformed log(x + 1) prior to analysis

DISCUSSION

Response patterns to floods of different magnitude

The results clearly indicate a response of the river biota to experimental flooding, both to each flood separately and to the cumulative impacts of previous floods. Because of its hypolimnetic release point for baseflow and flood flows, little chemical or temperature change was observed during each flood: thus, any observed changes in the biota probably were a function of the high flows on scouring, bedload transport and sheer forces (i.e. increased water velocities). For example, the suspended sediment data showed that fine material was mobilized during the rising limb of flood waters and remained mobile for a few hours following peak flow. Lawrence and Ward (1982) found a significant relationship between sediment release from a reservoir and decreases in macroinvertebrate abundances. We also found changes in stream profiles before and after each flood (data not shown), suggesting bed sediments were being both scoured and deposited. The physical changes in stream properties were translated in the immediate responses and short-term recoveries of biotic assemblages.

The first flood (15 June) was a relatively low-magnitude event, peaking at about ten times the residual baseflow. This flood was patchy in its effects on stream benthos, as evidenced by the high variance among initial post-flood zoobenthos samples. For example, the coefficient of variation (CV) among macroinvertebrate samples before the flood averaged 64% (range 40–85%), whereas samples collected the day after the flood had a CV of 148%. Indeed, we observed some areas of stream bed to be highly altered due to scouring and bed movement, resulting in a reduction in periphyton and zoobenthic standing stocks. Other patches of stream bed, and even larger substrate such as boulders, were less affected, perhaps even accumulating animals. Matthaei *et al.* (1999a,b) also found a high degree of patchiness in the effects of flood disturbance, some areas being scoured, others filled, and still others left unaffected. Palmer *et al.* (1995) showed that the impact of spates on macroinvertebrates was patch specific, although spates clearly caused a redistribution of taxa. The patchy nature of the first flood also was evident in the differential loss of moss coverage on stones (U. Uehlinger and C.T. Robinson, personal observation). Some stream

patches still had prolific growths of mosses that probably retained and provided refugia to organisms during this flood.

The second flood (5 July) was around 30 times higher than residual flows. This flood mobilized most areas of the stream bed and changed channel morphology (some pools were actually filled from the second flood), causing major reductions in periphyton biomass and zoobenthos density. For example, stream stones (including boulders) were essentially bare after this large flood and little moss was found in the main channel. Periphyton chlorophyll a concentrations decreased from 79 mg/m^2 before the flood to 0.37 mg/m^2 the day after the flood. The amount of benthic organic matter also was lower following this flood, a result not observed after the first flood. Indeed, the flood had similar effects as those observed following catastrophic flooding such as from spates in arid and prealpine environments (Badri et al., 1987; Grimm and Fisher, 1989; Uehlinger et al., 1996; Lytle, 2000). This similarity to catastrophic flooding is especially probable in confined rivers below reservoirs where lateral displacement of water is reduced relative to unconfined channels (e.g. Badri et al., 1987; but see Wondzell and Swanson, 1999). The abrupt flow increases by flooding also typically results in a major increase in drifting organisms (Irvine and Henriques, 1984; Imbert and Perry, 2000). For instance, the loss in zoobenthos primarily reflected major decreases in the abundance of chironomids and simuliids, taxa often found in the drift. This flood also caused a major decrease in gammarid abundance, as patches left undisturbed in the first flood were mobilized or scoured in the second larger flood. Numerous gammarids (and other taxa) were found stranded on the shoreline following the floods.

The third flood (10 August) was similar in magnitude to the first flood; however, recovery between the second large flood and this flood was less pronounced than recovery between the first and second floods. As a consequence, the third flood also reduced animal abundances and benthic organic matter, but little change was observed in periphyton standing crops. The third flood essentially reset biotic properties to levels found following the second flood. The differential impact of the large second flood relative to the third flood is best shown in the results of suspended sediment and seston sampled during the two floods. Although temporal patterns were similar in measured parameters during each flood, the large flood had three to four times the concentration of seston and orders of magnitude higher levels of suspended sediment than the third flood. Clearly, the scouring potential of the large flood may have had a major 'cleaning' effect, transporting many fines downstream thus reducing the amount of fine material available for transport and scour during the third flood. Assessing the effects and location of transported fines downriver is in need of additional study, especially over multiple years.

Flood magnitude obviously played an important role in dictating the kinds and amounts of refugia in the channels of streams (e.g. Cobb *et al.*, 1992). This is especially true in rivers below dams in which flows have been modified or maintained at a residual level for many years, with physical and biotic responses being related to flood magnitude and to the effects of previous floods of varying magnitudes. For instance, earlier floods may have increased the susceptibility of particular substrate patches to disturbance by later floods, perhaps by reducing the amount of fine sediments that can armour stream bottoms. The second flood in August was more intense than the other floods, probably disturbing areas that were refugia during the smaller floods, thus causing a reduction in sources of potential colonists. For example, Rempel *et al.* (1999) noted macroinvertebrates used shoreline areas as refugia in a large river that experienced annual high flows, but shorelines may act as traps in channels of regulated rivers by stranding a high number of animals once flows recede (Perry and Perry, 1986; C.T. Robinson, personal observation). As suggested by Peterson *et al.* (1994), recovery of benthos may be influenced by the degree of disturbance in concert with the timing from a previous disturbance and the composition of the community in response to previous floods.

Responses in community assembly: periphyton

Temporal shifts in community assembly, whether induced by seasonal changes in population life histories or by the differential loss or gain of taxa to earlier floods, may partially explain recovery processes following each flood. Periphyton biomass appeared to recover quickly after the first flood, although it was highly patchy as indicated by the four-fold increase in sample CVs. As mentioned, some patches of moss remained following the first flood, and some areas of stream bed appeared less disturbed than others (C.T. Robinson, personal observation). This patchy

effect of the first flood may have enhanced recovery by providing colonists or propagules. In unregulated systems, propagules from disturbance-resistant algae and macrophytes usually enhance recovery (e.g. Barrat-Segretain and Bornette, 2000). The timing of recovery (less than 30 days) is what would be expected following patchy disturbance (Robinson and Minshall, 1986; Resh *et al.*, 1988; Matthaei *et al.*, 1996). Rutherford *et al.* (2000) also noted that algal recovery may be enhanced following floods in summer because of reduced grazer populations, and algal recovery in frequently disturbed systems typically is rapid (Peterson *et al.*, 1994; Peterson, 1996; Uehlinger *et al.*, 1996). Consequently, we may expect similar response patterns of periphyton among different types of rivers following catastrophic disturbance, e.g. the River Spöl rarely experienced flood disturbance relative to systems that are more frequently disturbed.

Recovery following the larger 10 August flood, in contrast, was delayed and standing stocks never achieved preflood levels before the third flood. This lack of recovery may be related to the larger impact of the August flood (i.e. greater magnitude of disturbance over a larger proportion of the stream channel), the timing of the second flood (influence of seasonality on assemblage composition; Boulton *et al.*, 1992; Robinson *et al.*, 2000), or a change in the periphyton community due to the effects of the first flood (Peterson *et al.*, 1994). We did find a change in the relative abundance of certain algal groups in the Spöl between the first and second flood (U. Uehlinger and coworkers, unpublished data), and assemblages coarsely changed from a moss-dominated community to one dominated by diatoms and filamentous algae during the flood year (C.T. Robinson and U. Uehlinger, personal observation). Dodds *et al.* (1996) found recovery of periphyton to take two months following a large flood (>50 years return interval), and bed-moving spates have been associated with low periphyton standing crops in other systems (Biggs and Thomsen, 1995; Uehlinger *et al.*, 1996; Uehlinger, 2000). The reduction of moss in the main channel in this study may have reduced competition among different algae, providing both substrata and nutrients. For example, the large increase in periphyton standing crops in December was due to a bloom of *Hydrurus foetidus*, a common filamentous green alga in alpine streams in winter.

Responses in community assembly: macroinvertebrates

Shifts in community assembly following each flood and over time also were evident for the macroinvertebrates, and probably contributed to observed recovery processes. Catastrophic floods in natural rivers cause major reductions in macroinvertebrate abundance (Giller et al., 1991; Cobb et al., 1992; Lytle, 2000) as also suggested by the orders-of-magnitude increases in drift densities during floods (Irvine and Henriques, 1984; Perry and Perry, 1986; Imbert and Perry, 2000; Gayraud et al., 2000). Many of these drifting organisms end up downstream (Lytle, 2000), although many also accumulate in refugia or low-flow habitats such as shorelines (Gersich and Brusven, 1981; Winterbottom et al., 1997; Lancaster, 1999). Some taxa also demonstrate species-specific behavioural responses to changes in flow by actively entering the drift (Minshall and Winger, 1968; Hart and Finelli, 1999; Holomuzki and Biggs, 1999; Lancaster, 1999; Gayraud et al., 2000). In addition, Dobson et al. (2000) showed that some limnephilid larvae (non-drifters) actually abandon cases when buried by sediments, an energetically costly behaviour. One would expect even greater impacts of flood disturbance to macroinvertebrate assemblages of regulated rivers with more constant residual flows, as these systems typically are inhabited by taxa associated with streams with predictable and stable flows (Armitage, 1976, 1977; Wallace, 1990; Ward and Stanford, 1995; Oberdorff et al., 2001; Vinson, 2001). For instance, gammarids and turbellarians (both taxa of more stable kinds of streams) were predominant taxa in the Spöl the year before the floods, and both were reduced in abundance during the flood year, as were total density, biomass and taxonomic richness (also see Armitage, 1977).

Taxon-specific responses were found following the floods that reflected differences in species traits. For example, taxa typical of streams with more stable flows, such as the gammarids and turbellarians, showed reduced abundances and little recovery following the floods. Here, the turbellarian was greatly reduced after the first flood, whereas the gammarid recovered quickly following this low-magnitude flood but was greatly reduced by the second large flood. The difference probably is attributable to the fact that gammarids are strong swimmers and turbellarians must crawl to potential refugia. We believe that a reduction in potential refugia during the more catastrophic second flood, as evidenced by the extensive disturbance of the stream bed, was a major factor in the reduction of gammarids during the flood period. Other taxa with univoltine (or longer) life cycles, such as the stone-cased caddisfly *Allogamus auricollis*, also decreased following the floods, e.g. we observed dead *A. auricollis*

without cases or with damaged cases during and immediately after the floods. A contrasting pattern was observed for simuliids and chironomids, both of which showed relatively fast recovery following each flood. These taxa exhibit traits allowing quick recolonization of denuded habitats (Robinson and Minshall, 1986; Matthaei *et al.*, 1996), similar to species found in desert streams subject to frequent flooding (Fisher *et al.*, 1982; Boulton *et al.*, 1992). Baetids, another taxon well-known for its dispersal ability (Mackay, 1992; Robinson *et al.*, 1993), also appeared highly resilient to the multiple floods.

Whether the observed change in community assembly (*sensu* Belyea and Lancaster, 1999) is maintained would require a longer observation period with a sustained artificial flood regime. Because of the multiple sources and pathways for recolonists, a change in habitat conditions, brought about by annual artificial floods, would be required to sustain a community assembly pre-adapted to a more variable flow regime, similar to assemblages in unregulated rivers. It is not apparent whether the macroinvertebrate assemblage in the Spöl is still in recovery to pre-flood 'flow-regulated' composition, or is perhaps in a state of transition. We suggest that the benthic community is still in 'non-equilibrium' with the new habitat templet (*sensu* Southwood, 1988). For instance, a number of taxa showed high abundances on the final sampling date in December, especially plecopterans, chironomids, baetids and simulids. Certainly, studies lasting longer than the life cycles of most taxa, perhaps including multiple generations, must be completed before this question can be answered.

CONCLUSIONS

In summary, experimental flooding significantly influenced benthic algae and macroinvertebrates in the River Spöl. Flood magnitude, as well as flood timing, had different effects on benthic assemblages. Flow is an integral component of river habitats and changes in flow (flood or drought) can be an important disturbance to riverine flora and fauna. Changes in the natural flow regime, such as by flow regulation below dams and water abstraction, can substantially alter species assemblages in downstream receiving waters. Our results indicate that multiple artificial floods can be used to influence instream habitat conditions, and thereby potentially change communities to a more natural composition. Additional studies are required to determine the long-term consequences of experimental flooding, especially regarding their timing and magnitude in relation to the extant community composition. Our results suggest that floods of similar magnitude may have different effects depending on the previous flood history and the seasonal changes in organism life histories.

ACKNOWLEDGEMENTS

We greatly appreciate the assistance and advice from personnel of the Swiss National Park, especially Thomas Scheurer and Flurin Filli. Field assistance was kindly provided by Christa Jolidon, Johannes Ortlepp, Ute Mürle, Mäggi Hieber, Stefan Aebischer, Christian Jakob, Michael Döring, Dimitry van der Nat, and Peter Burgherr. We especially thank Richard Illi for completing the chemical and chlorophyll analyses, Christa Jolidon for processing the numerous benthic samples, and Mäggi Hieber for assistance with periphyton samples. The comments by an anonymous reviewer helped clarify the text and brought to our attention some additional literature on flushing flows. Partial support for the study was provided by the Swiss National Park.

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