

Feature Article

Longitudinal effects of experimental floods on stream benthos downstream from a large dam

Christian Jakob¹, Christopher T. Robinson^{2,*} and Urs Uehlinger²

¹ Zoologisches Institut, Universität Zürich, CH-8057 Zürich, Switzerland

² Department of Limnology, EAWAG/ETHZ, CH-8600 Dübendorf, Switzerland

Received: 10 March 2003; revised manuscript accepted: 12 May 2003

Abstract. We examined the longitudinal effects of 3 experimental floods on seston, periphyton, and macroinvertebrates in a regulated river downstream from a large reservoir in the Swiss Alps. In addition, suspended organic sediments, in conjunction with conductivity and turbidity, were measured during each flood. Three study reaches were selected downstream from the reservoir: an Upper site ca 150 m, a Middle site at 1.2 km, and a Lower site at 2.3 km from the dam. The Upper site was located upstream of any significant source of sediments. No flood effect was observed on water temperature, although river temperatures and diel amplitudes increased progressively downstream from the dam. Most organic sediments were mobilized and transported within the first few hours of each flood, with the pulse in sediments typically occurring later (after peak discharge) and being more prolonged at the Lower site. Turbidity generally decreased

during the flood season, perhaps in response to lower amounts of fines and reductions in periphyton biomass. Seston concentrations (as chlorophyll a and AFDM) were lowest at the Upper site, and typically decreased following each flood. The flood response in seston was lowest at the Upper site and more pronounced at the Middle and Lower sites. Periphyton biomass also was lowest at the Upper site, and the flood effects were significant only in the Middle and Lower sites. In contrast, macroinvertebrate densities were similar between the Upper and Lower sites, and both sites exhibited a similar response to the floods. These results indicate a longitudinal response of river benthos to flooding below the reservoir that partly reflects the examined benthic constituent (periphyton or zoobenthos) and the longitudinal differences in the degree and type (e.g., flow in combination with sediment mobility and scouring) of disturbance.

Key words. Flow regime; periphyton; macroinvertebrates; serial discontinuity; disturbance.

Introduction

The effects of dams on downstream receiving waters have been well-documented (Ward and Stanford, 1979; Giller and Malmqvist, 1998; Friedl and Wüest, 2002). Regulated rivers below dams experience altered conditions in water chemistry, temperature, sediment load, discharge, and flow regime. As a consequence, dams affect stream channel morphology via, e.g., colmation and armouring

by fine sediments, or channel confinement by debris fans extending into the river and bed aggradation (Cobb et al., 1992). High elevation dams in the Alps impose additional impacts on downstream rivers because in many cases the water is diverted from the reservoir to downstream energy production facilities (Petts and Bickerton, 1994). As a result, these rivers receive only a small and constant residual discharge. This is in contrast to the natural flow regime of Alpine streams where periodic floods and seasonal flow patterns play a crucial role in their structure and function. Floods in these systems act as a disturbance, an important component of the habitat template dictating the composition of benthic assemblages (Ward

* Corresponding author phone: +41 1 823 53 17;
fax: +41 1 823 53 15; e-mail: robinson@eawag.ch
Published on Web: September 23, 2003

and Stanford, 1983; Resh et al., 1988; Townsend et al., 1997). In regulated streams below large dams, the absence of floods, in combination with altered physical and chemical conditions, also lead to dramatic changes in biotic assemblages (Ward and Stanford, 1979; Vinson, 2001). In general, biodiversity in streams below dams tends to be lower than in natural streams because assemblages are made up of a few very abundant taxa due to the more constant habitat conditions (Pringle et al., 2000; Vinson, 2001). Typically, non-insect taxa, such as gastropods, amphipods and turbellarians, benefit from these altered conditions.

According to the Serial Discontinuity Concept (Ward and Stanford, 1983; 1995), the position of a dam on the longitudinal river profile determines its impact on the ecology of downstream waters. Generally, this concept suggests that the ecological effects of dams on rivers decreases with increasing distance from the dam, depending on sediment availability and inputs from tributaries. For instance, the first major tributary entering our study river (Spöl River) is around 5.5 km downriver from the dam, although it flows directly into the next reservoir in this system. Similarly, one would expect the effects of artificial floods to also change longitudinally downstream from the dam. For example, sediment supply and mobility may increase downstream as contributions from side-slopes and tributaries increase. Near the dam, disturbance may simply be from sheer stress associated with higher flows, whereas the effects of sediment scouring probably increases further downstream (Shannon et al., 2001). For instance, the first lateral debris flow into the Spöl River occurs around 250 m below the dam, thus disturbance by sediment scouring is probably minimal upstream of this debris flow.

The restoration of the natural flow regime to regulated rivers to improve their ecological integrity has been a relatively recent phenomenon (Stanford et al., 1996; Poff et al., 1997; Michener and Haeuber, 1998). Single periodic floods (flushing flows) have been frequently used to remove fine sediments that accumulate in reaches below dams with the primary intent to improve habitat conditions and fisheries (see references in Reiser et al., 1985). Most notable of such a single high flow was the Glen Canyon flood experiment on the Colorado River below lake Powell (Andrews and Pizzi, 2000), even-though that experiment was designed to mobilize and redistribute sediments rather than as a pure flushing flow. However, there have been only a handful of studies addressing the use of sequential floods (intra-annual and annual) for river restoration (Rulifson and Manooch, 1993; Molles et al., 1998; Robinson et al., 2003). Although incorporated into the Glen Canyon flood study (Shannon et al., 2001; Valdez et al., 2001), few other studies have examined the longitudinal effects of experimental floods below large dams. Here we report on the longitudinal effects of three

floods on stream benthos in the River Spöl downstream from the Livigno Reservoir. Readers are referred to Scheurer and Molinari (2003) for specific details of the flood program.

Methods

Site description

The Spöl is a canyon-confined river flowing through the Swiss National Park in southeastern Switzerland. It originates from the Livigno reservoir (Lago di Livigno) resulting from the Punt dal Gall dam (46°37'20"N, 10°11'30"E) on the Swiss-Italian border (Fig. 1). The Spöl watershed covers 295 km². The elevation of Lago di Livigno is 1805 m a.s.l. Below the dam, the Spöl flows 5.5 km before entering the Ova Spin reservoir at an elevation of 1630 m a.s.l. From this reservoir, the Spöl flows another 5.5 km to its confluence with the Inn River, a major tributary to the Danube, in the lower Engadine at Zernez.

Construction of the dam was completed in 1970 with a reservoir capacity of 1.64×10^8 m³. The dam itself is a double-arch dam, 130 m high and 540 m wide. Most of the water from Livigno reservoir is transferred through a 7.6 km pressure tunnel to the power plant below the Ova Spin reservoir. As a consequence, the Spöl's discharge was reduced from 6–12 m³/s (peak flows up to 120 m³/s) before regulation to a constant residual flow of 1.45 m³/s in summer and 0.55 m³/s in winter. Documented physical effects on the river included lateral debris fans entering the channel with upstream shallow water zones, deposition of fine sediments that silted the riverbed, general homogenization of aquatic habitats, river aggradation, colonization of trees on the stream bank and on gravel terraces, an increase in disturbance-intolerant species, and an increase in mosses and filamentous algae in the river (Rey and Gerster, 1991; Scheurer, 2000).

In cooperation with the Swiss National Park and the Engadiner Kraftwerke Power Company, three artificial floods of different magnitude were released in June, July and August 2000–2001. In each year, two floods around 10 m³/s (release time of 6 to 8 hours) were implemented in June and August, and one larger flood around 30 m³/s (release time of 7 to 9 hours) done in July. Scheurer and Molinari (2003) describe the history, design, goals, and implementation of the flood program. Discharge was recorded at the reservoir by the Swiss Federal Office of Water and Geology. The present study was completed in the 2001 flood year. Study sites were located ca 150 m (Upper site), 1.2 km (Middle site), and 2.3 km (Lower site) downstream of the dam (Fig. 1). Table 1 provides a physical and chemical description for each study site.

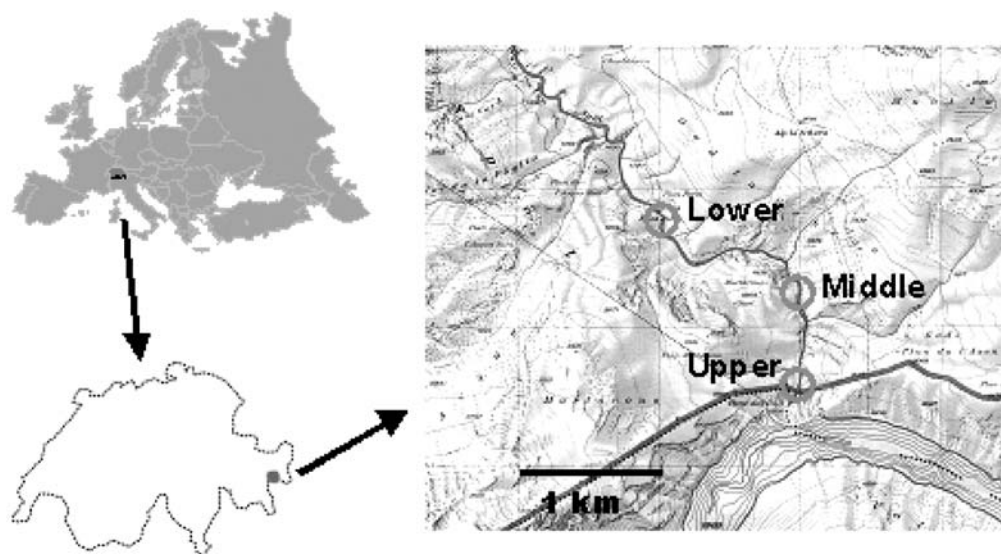


Figure 1. Map showing Europe, Switzerland and the location of the three study sites on the River Spöl in the Swiss National Park downstream of Punt dal Gall dam that forms Livigno reservoir in Italy.

Table 1. Chemical, physical and morphological characteristics of the study sites. Data represented as the mean and coefficients of variation (CV) from samples collected periodically during the study. N = 13 for chemical measures, except n = 12 for the Middle site. DOC = dissolved organic carbon, TIC = total inorganic carbon and POC = particulate organic carbon.

Parameter		Upper	Middle	Lower
NO ₂ +NO ₃ (µg/l)	Mean	272	257	231
	CV	7.4	5.6	8.1
PO ₄ -P (µg/l)	Mean	0.7	0.3	0.5
	CV	180	150	109
DOC (mg/l)	Mean	0.8	0.8	0.8
	CV	22	21	21
TIC (mg/l)	Mean	21.8	21.6	23.2
	CV	4.9	3.4	5.1
POC (mg/l)	Mean	0.5	0.4	0.4
	CV	45	36	55
Substrate size (cm)	Mean	12	13	20
	CV	41	40	61
Near-bed velocity (m/s)	Mean	0.61	0.77	0.63
	CV	56	52	63
Slope (%)		0.9	1.8	0.7

Sampling during each flood

Water samples (0.5–1 litre) were taken during each flood at regular intervals, ranging from 30 min (early period of flooding) to 1 or 2 h (later period of flooding) for estimates of suspended organic sediments. Samples were filtered (Whatman GF/F filters) and analysed as ash-free dry mass (AFDM). Each sample was oven-dried at 60 °C, weighed, combusted at 500 °C, and then reweighed for determination of AFDM. In addition, turbidity (nephelo-

metric turbidity units, NTU; Cosmos, Züllig AG, Switzerland) and conductivity (WTW meter, model LF 323, Weinheim, Germany) were recorded manually using portable meters.

Field protocols

Benthic and water samples were collected at 3–4 week intervals at each site during the study. The collection period ran from May through November because of poor accessibility in winter. In addition to these periodic samples, collections also were made immediately before and after each flood. Water temperature was recorded at each site using temperature loggers (StowAway™ XTI, Onset Corp., USA). Conductivity and turbidity were recorded with portable meters on each visit at each site. On each visit, we collected a 1-L water sample for chemical analysis in the laboratory. In the laboratory, aliquots from each water sample were filtered (Whatman GF/F filters) and then analysed for particulate organic carbon (POC), nitrate (NO₂+NO₃), phosphate (PO₄-P), dissolved organic carbon (DOC) and total inorganic carbon (TIC) following methods described in Tockner et al. (1997). Slope was determined for each site using a clinometer. In addition, the b-axis (width) of 50–70 randomly collected stones were measured and near-bed velocities (MiniAir 2, Schiltknecht, Switzerland) recorded at these same locations at each site.

Seston samples (n = 3) were taken on each visit at each site using a 1-m long net (100 µ mesh, aperture 11 cm). Water velocity at the net mouth was measured with a velocity meter and used to calculate the volume of water filtered. Nets were deployed between 2–3 minutes depend-

ing on clogging. Each sample was stored in whirl-pac bags and frozen at -25°C until processing. In the laboratory, each sample was filtered through a pre-ashed (450°C) Whatman GF/F filter. Each filter was then cut in half, with one half used for determination of ash-free dry mass (AFDM) and the other for chlorophyll a (Murray et al., 1986; DEV, 1986).

Periphyton biomass was assessed from 10 randomly collected rocks from each site on each visit. Rocks were placed in plastic storage bags and kept frozen at -25°C until processed. In the laboratory, each stone was scrubbed using a metal bristle brush and rinsed to remove all visible signs of periphyton. If moss was present on a rock it was removed before periphyton analysis. Two measured aliquots of the periphyton slurry from each rock were filtered (Whatman GF/F filters). One filter was used for determination of AFDM and the other for chlorophyll a with values expressed per unit stone area (Uehlinger, 1991; Donath and Robinson, 2001).

Benthic macroinvertebrates were collected from riffle/run habitats ($n = 3$) at each site on each sampling date using a modified Hess sampler (0.045 m^2 , $100\ \mu$ mesh). Samples were stored in plastic bottles and preserved in the field with 70% ethanol. Macroinvertebrates were hand-picked from each sample, counted and determined to lowest possible taxonomic level (usually genus) using a Leica microscope. Samples with a large number of animals ($>20,000$ individuals/ m^2) were subsampled following Meyer (1990). Two-way ANOVA (site and date) followed by Tukey's HSD (honest significant difference) post-hoc test was used to compare seston, periphyton, and macroinvertebrate parameters (Zar, 1984). Data were transformed $\log(n+1)$ to improve homoscedasticity prior to analysis (Zar, 1984).

Results

Physical-chemical responses

There was no effect of the floods on stream temperature. All three sites showed a slight increase in minimum daily temperature from mid-May to late-August with the progression of summer, and maxima and daily amplitudes increased with increasing distance from the dam. Conductivity values typically decreased by up to 10 percent during each flood (data shown for the July flood, Fig. 2), recovering quickly once release waters were terminated. A sharp turbidity peak of short duration (ca. 60–120 minutes) occurred during flood rise at the Upper site and shortly preceded maximum discharge at the Lower site (data shown for the June flood, Fig. 2). There also was a small second turbidity increase at the Lower site, probably due to a secondary pulse of sediment release. Turbidity values usually returned to base levels within 2 hours during each flood. Ash-free dry mass values for sus-

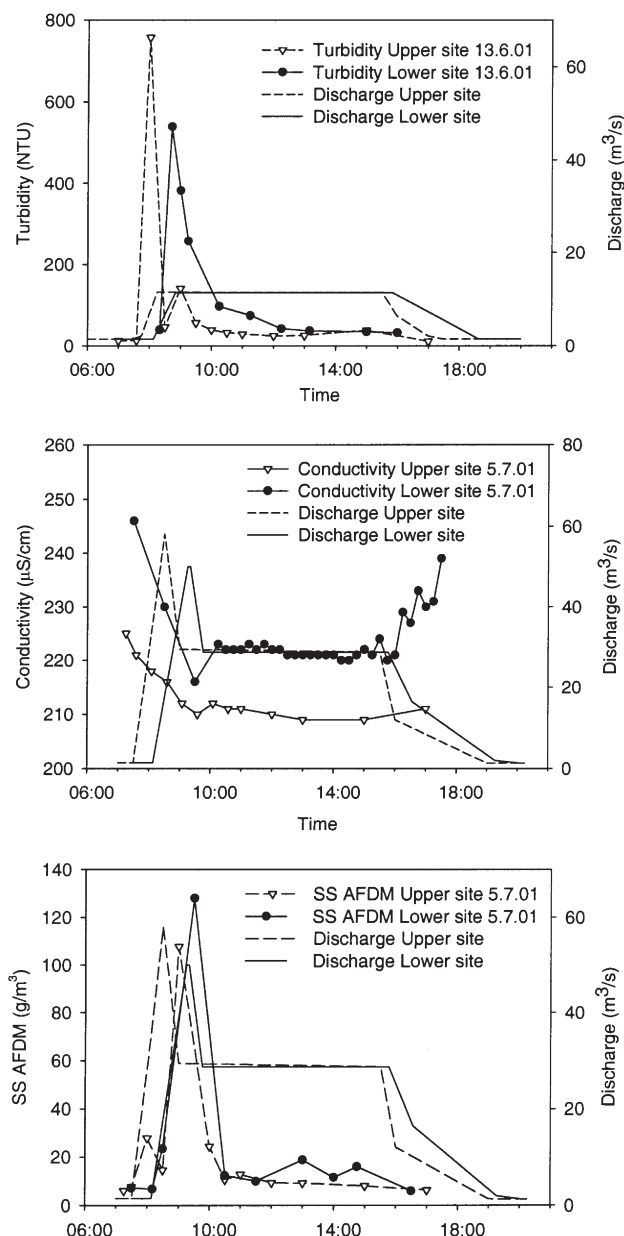


Figure 2. Changes in turbidity (NTU), conductivity and suspended sediments (SS as AFDM) during selected floods plotted with respective discharges. Data were collected only for the Upper and Lower sites during each flood. Turbidity is shown for the June flood and conductivity and SS for the July flood.

pended sediments (SS) followed the same pattern as turbidity (Fig. 2). During the June flood, for example, the maximum peak for SS at the Upper site (50.2 g/m^3) occurred just after attainment of maximum discharge. The SS peak was smaller (27.9 g/m^3) and happened at about the same time as maximum discharge at the Lower site (data not shown). At the Lower site in July, the peak in SS also occurred at about the same time as maximum discharge, but the SS peak was higher (128 g/m^3) at the Lower site than the Upper site (108 g/m^3) (Fig. 2).

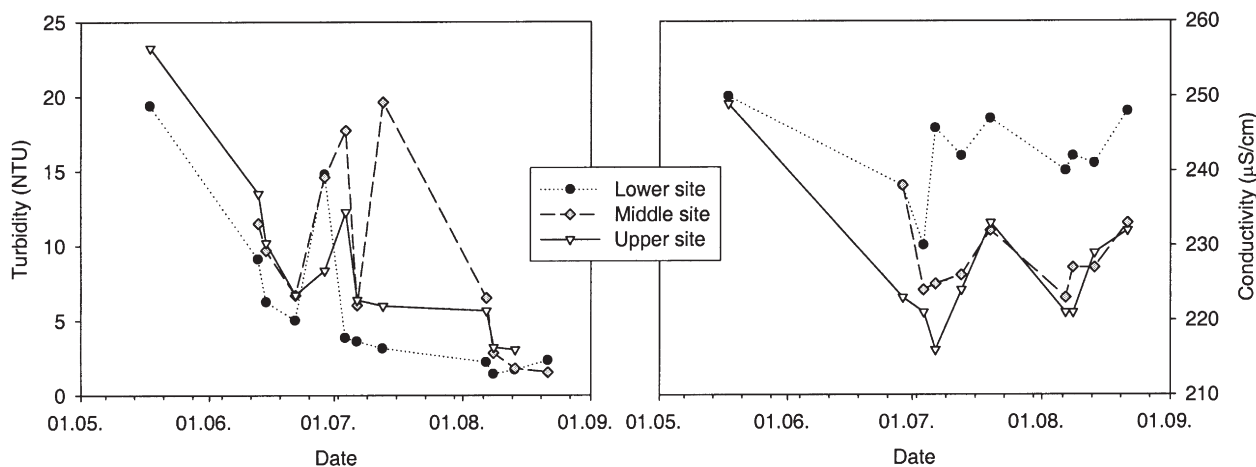


Figure 3. Temporal patterns in turbidity and conductivity for each site during the study period. Data recorded in the field with portable meters during each respective visit.

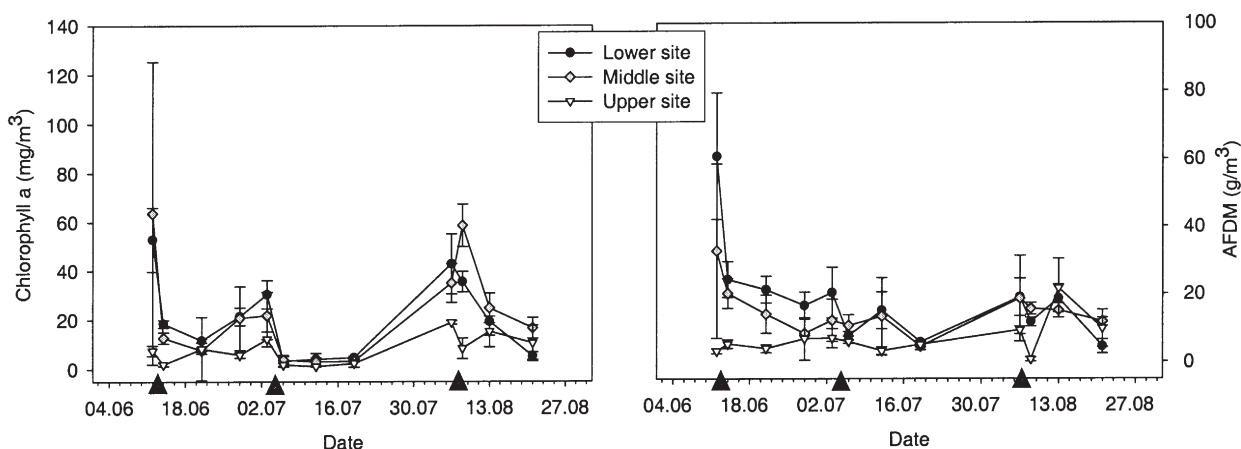


Figure 4. Temporal patterns in seston as chlorophyll a and ash-free dry mass (AFDM) at each site during the study. Symbols are means ± 1 SD ($n = 3$). Triangles indicate the time of each flood.

In general, turbidity decreased at all 3 sites over the study period in 2001 (Fig. 3). A turbidity peak was visible in late June at each site resulting from side-slope inputs of fine sediments during a rainy period. The Upper site showed the least response to this rain effect, whereas the Middle, in particular, and Lower sites both showed more dramatic effects. Conductivity showed an inverse spatial pattern of turbidity (Fig. 3). Values typically were highest at the Lower site with similar and lower values at the Middle and Upper sites. The rain influence was again visible with conductivity decreasing by 5% at each site (Fig. 3).

Response in seston

Seston, as chlorophyll a (chl a), chlorophyll b (chl b, data not shown) and AFDM, was significantly different among sites and date (chl a: $F = 3.4$, $p < 0.0001$, chl b:

$F = 2.2$, $p < 0.0006$, AFDM: $F = 16.5$, $p < 0.0001$) (Fig. 4). Tukey's post-hoc comparison test indicated a significant decrease in seston before and after the June flood at the Middle and Lower sites for chl a ($p < 0.05$), and at the Middle site for chl b ($p < 0.05$). No significant differences in seston (all parameters) were found before and after the July flood, although seston AFDM was reduced significantly by the August flood at the Middle site ($p < 0.05$). Seston values were not affected significantly at the Upper site by any of the floods (Fig. 4).

Response in periphyton

Two-way ANOVA indicated a significant site and date effect on periphyton parameters (chl a: $F = 4.3$, $p < 0.0001$, chl b: $F = 3.6$, $p < 0.0001$ (not shown), AFDM: $F = 4.2$, $p < 0.0001$) (Fig. 5). Tukey's post-hoc test showed significant ($p < 0.05$) decreases in periphyton AFDM after the

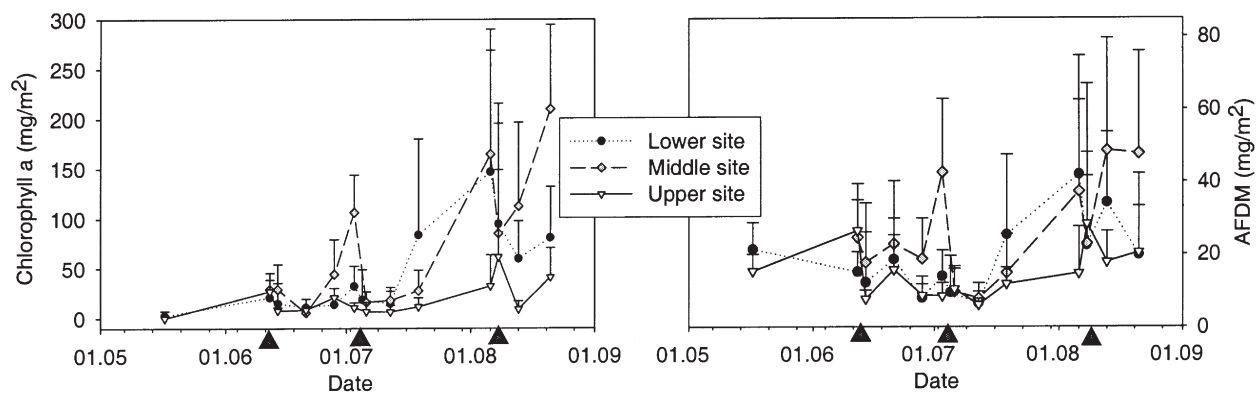


Figure 5. Temporal patterns in periphyton biomass (as chlorophyll a and AFDM) collected from 10 rocks at each site on each date. Symbols are means +1 SD. Triangles indicate the time of each flood.

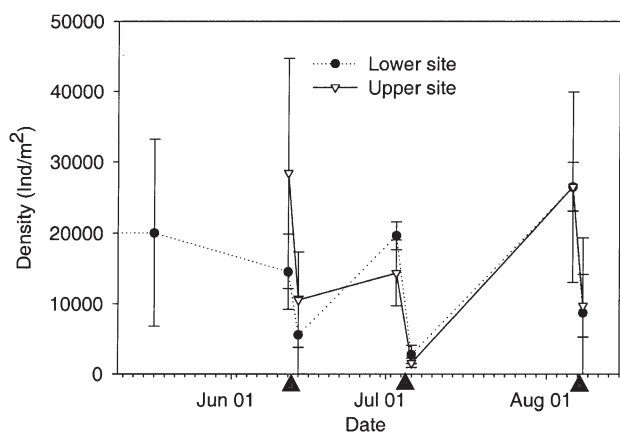


Figure 6. Mean macroinvertebrate densities (ind./m² ± 1 SD) at the Upper and Lower sites sampled at periodic times during the study period (n = 3). Triangles indicate the time of each flood.

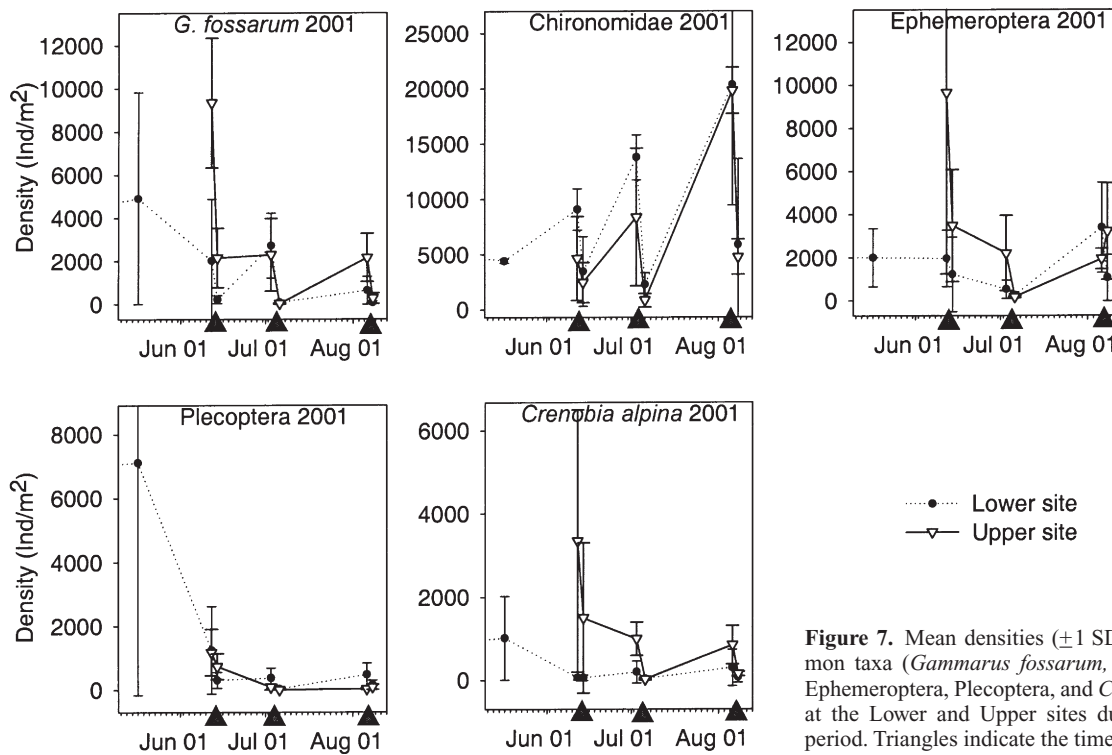


Figure 7. Mean densities (± 1 SD) of five common taxa (*Gammarus fossarum*, Chironomidae, Ephemeroptera, Plecoptera, and *Crenobia alpina*) at the Lower and Upper sites during the study period. Triangles indicate the time of each flood.

June flood at the Upper site. Significant differences were evident before and after the July flood at the Middle site (for chl a and AFDM) and at the Lower site (chl a).

Response in macroinvertebrates

Macroinvertebrate densities were analyzed before and after each flood only for the Upper and Lower sites (Fig. 6). Two-way ANOVA showed significant differences among dates ($F = 9.6$, $p < 0.0001$), but not between sites ($F = 1.0$, $p = 0.3$) or for the interaction term ($F = 0.9$, $p = 0.5$). Tukey's test indicated significant differences in density only before and after the July flood ($p < 0.05$), although average densities were lower after each flood (Fig. 6). Macroinvertebrates, in terms of overall density, recovered within a matter of weeks after each flood. Taxonomic richness also was reduced significantly by the floods (data not shown).

The densities of the five most common taxa (*Gammarus fossarum* (Amphipoda: Gammaridae), Chironomidae, Ephemeroptera, Plecoptera (including Nemouridae and Leuctridae), and *Crenobia alpina* (Tricladida: Planariidae) at the Upper and Lower sites are shown in Figure 7. The various taxa displayed different recovery patterns following the floods, see for example, Chironomidae response versus that of *Crenobia alpina*. Tukey's post-hoc test showed that only the large July flood had a significant effect on the density of *G. fossarum* and Chironomidae. *Crenobia alpina* was affected by the July flood at the Upper site, but not at the Lower site. Lastly, two-way ANOVA indicated a significant date effect on total macroinvertebrate density ($F = 2.9$, $p = 0.04$), but no significant site ($F = 0.4$, $p = 0.5$) or interaction ($F = 0.5$, $p = 0.8$) effects (data not shown).

Discussion

This study was designed to examine the longitudinal effects of flooding on a river downstream of a large impoundment. We observed a variety of responses depending on the parameter of interest. No effect was found on water temperature because the dam is a deep release reservoir, thus releasing relatively cool and constant water. The major longitudinal effects were an increase in average temperature by a few degrees and an increase in diel amplitude with distance from the reservoir due to longer exposure to air temperatures and solar radiation. Conductivity values simply changed in response to the degree of influence of the flood waters. As flood waters receded, the influence of other water sources caused conductivity levels to return to background concentrations.

Turbidity (and similarly suspended sediments) increased at the Upper site during the June flood mainly from the input of lake sediments, as this site was ca 150

m downstream of the dam. The lake sediments were quickly flushed and turbidity thus decreased before the maximum flood discharge (Gerster and Rey, 1994). At the Lower site, maximum turbidity was reached at the same time as maximum discharge for several reasons: slower transport velocities, greater scouring with higher discharge, and the rising water added sediments and debris from riparian areas. These various effects of high discharge with distance caused the turbidity peak to be relatively lower but longer at the Lower site than at the more upstream locations. A similar pattern in turbidity was observed during the August flood, although peak levels were around 40% lower as the lake sediments appeared to be flushed from the previous floods. Further, peak turbidity levels were about 23% lower at the Lower site than at the Upper site in August, suggesting that much of the fine sediments in the Spöl had been flushed by the earlier two floods. However, no long-term effects were noted for the above physical and chemical measures due to the floods.

Seston (as chlorophyll a and AFDM) collected during the June flood at the Upper site was low. Lake derived plankton also had little effect on total seston values, as high seston levels were maintained only briefly and returned rapidly to background levels at the Upper site. In general, the Upper site had much lower seston levels compared to the Middle and Lower sites. Seston consisted mainly of coarse particulate organic matter derived from the river channel and the stream banks as water levels increased. Seston chlorophyll values decreased significantly the day after the floods at the Middle and Lower sites probably because of the major scouring of periphyton from the river bed. The higher discharge of the July flood resulted in an even greater scouring capacity and a 4–5 times higher seston load at the Lower site than at the Upper site. However, an abundance of *Hydrurus foetidus* (a filamentous algae) at the Upper site before the August flood (C. Jakob, pers. observ.) resulted in high seston values during that flood as this alga was easily scoured from the stream bed. Further downstream, the river channel and stream banks were already flushed by the large July flood and thus had little additional organic matter for transport.

The present study showed that both flood magnitude and the longitudinal distribution of the study sites played an important role in the effects of the floods on periphyton. For example, the effects of flooding on periphyton biomass were significant only for the large July flood, when substantial scouring was evident at the Middle and Lower sites in particular. There also was a major decrease in periphyton AFDM at the Upper site after the June flood, although no effect was seen in periphyton chlorophyll concentrations. Others have noted that flood frequency is related negatively to periphyton chlorophyll abundance (Biggs, 1995), although this relationship occurs only if the algae are scoured (Shannon et al., 2001).

Little scouring material was present at the Upper site because of its proximity to the dam, and essentially no new material is delivered from valley side-slopes upstream of the Upper site. Side-slope inputs increase longitudinally downstream from the dam, thus increasing the scouring potential at downstream sites. Further, periphyton supposedly recovered more slowly at the Upper site possibly due to a lack of recolonization from upstream sources because of its proximity to the dam.

Macroinvertebrates (in numbers and richness) were affected by the floods at all three sites, and there was a significant effect of seasonality on taxon richness at all sites. Despite some taxa disappearing or becoming rare at the Lower site, however, no major long-term effects of the floods in 2001 were apparent. Further, although average numbers decreased after each flood, only the large July flood had a significant effect on total macroinvertebrate density at the study sites. The immediate flood effects on the densities of some common taxa also were significant for the July flood, although even here some taxa were unaffected by the flood. The July flood significantly decreased the abundance of *Gammarus fossarum* and Chironomidae at the study sites, as well as the turbellarian *Crenobia alpina* at the Upper site. The Chironomidae, in particular, are known to drift in response to flood disturbance (Wallace, 1990). *Crenobia alpina*, which was more abundant at the Upper than at the Lower site, perhaps because of its upstream migration behavior, is a taxon well-adapted to more constant habitat conditions and is limited in mechanisms for escaping increasing current (Hynes, 1970; Pennak, 1978). The amphipod *Gammarus fossarum* is another example of a taxon ill-adapted to fast running waters, showing current-avoidance by hiding under stones or in patches of macrophytes or mosses. Typically, this taxon is flushed when the current velocity increases with flooding.

The Ephemeroptera and Plecoptera showed no significant response to any of the floods, they being morphologically better adapted to higher flow velocities with good agility/mobility, attachment ability (hooks, claws) and behavior patterns (e.g., *Leuctra* spp. burrow into gravel to avoid high currents and were a common stonefly in the Spöl). The importance of behavioral responses to flooding has been shown by Holomuzki and Biggs (2000). Trichoptera abundance decreased to near-zero for both the Rhyacophilidae and Limnephilidae at the Lower site (in contrast to the Upper site). Many destroyed and empty caddis cases were found following the floods (especially the July flood), indicating major disturbance by scouring and stone tumbling at the lower sites. This degree of disturbance was not observed at the Upper site, as the availability of fine sediment for transport was minimal. In contrast to periphyton, it was clear that the longitudinal effect of the floods was less pronounced for macroinvertebrates. For instance, those macroinverte-

brate taxa ill-adapted to high flows or increases in velocity were susceptible to flood disturbance regardless of longitudinal position downstream of the dam. In conclusion, our results support the general premise that the effects of artificial floods downstream of dams are related to the longitudinal changes in flow (shear stress) and sediment mobility (scouring and transport) associated with high flow disturbance and the consequent effects on specific riverine flora and fauna.

Acknowledgments

We thank M. Hieber, M. T. Monaghan and S. Aebischer for assistance in the field, and G. Meier-Buergisser and R. Illi for analyzing the water chemistry samples. We thank F. Filli and T. Scheurer for logistical support and advice during the project. We thank T. R. Angradi, T. V. Royer, and M. Vinson for constructive comments on the manuscript. Partial support was provided by the Swiss National Park.

References

- Andrews, E. D. and L. A. Pizzi, 2000. Origin of the Colorado River experimental flood in Grand Canyon. *Hydrolog. Sci. J.* **45**: 607–627.
- Biggs, B. J. F., 1995. The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. *Freshwat. Biol.* **33**: 419–438.
- Cobb, G. C., T. D. Galloway and J. F. Flannagan, 1992. Effects of discharge and substrate stability on density and species composition of stream insects. *Can. J. Fish. Aq. Sci.* **49**: 1788–1795.
- DEV, 1986. Deutsche Einheitsverfahren zur Wasseruntersuchung. Verlag Chemie, Weinheim.
- Donath, U. and C.T. Robinson, 2001. Ecological characteristics of lake outlets in alpine environments of the Swiss Alps. *Arch. Hydrobiol.* **150**: 207–225.
- Friedl, G. and A. Wüest, 2002. Disrupting biogeochemical cycles – Consequences of damming. *Aquat. Sci.* **64**: 55–65.
- Gerster, S. and P. Rey, 1994. Ökologische Folgen von Stauraumpülungen. Bundesamt für Umwelt, Wald und Landschaft.
- Giller, P. S. and B. Malmqvist, 1998. The biology of streams and rivers. Oxford University Press, Oxford, New York, Toronto.
- Holomuzki, J. R. and B. J. F. Biggs, 2000. Taxon-specific responses to high-flow disturbance in streams: implications for population persistence. *J. N. Am. Benthol. Soc.* **19**: 670–679.
- Hynes, H. N. B., 1970. The ecology of running waters. University of Toronto Press, Toronto.
- Meyer, E., 1990. A simple subsampling device for macroinvertebrates with general remarks on the processing of stream benthos samples. *Arch. Hydrobiol.* **117**: 309–318.
- Michener, W. K. and R. A. Hauber, 1998. Flooding: natural and managed disturbances. *BioScience* **48**: 677–680.
- Molles, M. C., C. S. Crawford, L. M. Ellis, H. M. Valett and C. N. Dahm, 1998. Managed flooding for riparian ecosystem restoration. *BioScience* **48**: 749–756.
- Murray, A. P., C. F. Gibbs, A. R. Longmore and D. J. Flett, 1986. Determination of chlorophyll in marine waters: intercomparison of rapid HPLC method with full HPLC, spectrophotometric and fluorometric methods. *Mar. Chem.* **19**: 211–227.

- Pennak, R. W., 1978. Freshwater invertebrates of the United States. John Wiley and Sons, New York.
- Petts, G. E. and M. A. Bickerton, 1994. Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. *Freshwat. Biol.* **32**: 375–386.
- Poff, N. L., J. D. Alan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks and J. C. Stromberg, 1997. The Natural Flow Regime. *BioScience* **47**: 769–784.
- Pringle, C. M., M. C. Freeman and B. J. Freeman, 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. *BioScience* **50**: 807–823.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace and R. C. Wissmar, 1988. The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.* **7**: 433–455.
- Rey, P. and S. Gerster, 1991. Wissenschaftliche Begleitung Spülung Grundablass Livigno-Stausee vom 7. Juni 1990 (4): Makroinvertebraten und Fische. Wissenschaftliche Nationalparkkommission, Konstanz und Bern.
- Robinson, C. T., U. Uehlinger and M. T. Monaghan, 2003. Stream ecosystem response to multiple experimental floods from a reservoir. *River Research and Applications*. **19**: 1–19.
- Rulifson, R. A. and C. S. Manooch, 1993. Roanoke River water flow committee report for 1991–1993. Albemarle-Pamlico estuarine study. Project No. APES 93–18, US EPA, Raleigh, North Carolina.
- Scheurer, T., 2000. Mehr Dynamik im Spöl. *Cratschla* **2/00**: 2–9.
- Scheurer, T. and P. Molinari, 2003. Experimental floods in the River Spöl, Swiss National Park: Framework, objectives and design. *Aquat. Sci.* **65(3)**: 183–190.
- Shannon, J. P., D. W. Blinn, T. McKinney, E. P. Benenati, K. P. Wilson and C. O'Brien, 2001. Aquatic food base response to the 1996 test flood below Glen Canyon Dam, Colorado River, Arizona. *Ecological Applications* **11**: 672–685.
- Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich and C. C. Coutant, 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management* **12**: 391–413.
- Tockner, K., F. Malard, P. Burgherr, C. T. Robinson, U. Uehlinger, R. Zah and J. V. Ward, 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem. *Arch. Hydrobiol.* **140**: 433–463.
- Townsend, C. R., M. R. Scarsbrook and S. Dolédec, 1997. The intermediate disturbance hypothesis, refugia and biodiversity in streams. *Limnology and Oceanography* **42**: 938–949.
- Uehlinger, U., 1991. Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Arch. Hydrobiol.* **128**: 39–55.
- Valdez, R. A., T. L. Hoffnagle, C. C. McIvor, T. McKinney and W. C. Leibfried, 2001. Effects of a test flood on fishes of the Colorado River in Grand Canyon, Arizona. *Ecol. Appl.* **11**: 686–700.
- Vinson, M. R., 2001. Long-term dynamics of an invertebrate assemblage downstream from a large dam. *Ecol. Appl.* **11**: 711–730.
- Wallace, J. B., 1990. Recovery of lotic macroinvertebrate communities from disturbance. *Environ. Manage.* **14**: 605–620.
- Ward, J. V. and J. A. Stanford, 1979. The ecology of regulated streams. Plenum Press, New York.
- Ward, J. V. and J. A. Stanford, 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pages 347–356 in T. D. Fontaine and S. M. Bartell, eds. *Dynamics of lotic ecosystems*. Ann Arbor Science, Ann Arbor.
- Ward, J. V. and J. A. Stanford, 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers* **11**: 105–119.
- Zar, J. H., 1984. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.



To access this journal online:
<http://www.birkhauser.ch>
