

EXPERIMENTAL FLOODS CAUSE ECOSYSTEM REGIME SHIFT IN A REGULATED RIVER

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Abstract. Reservoirs have altered the flow regime of most rivers on the globe. To simulate the natural flow regime, experimental floods are being implemented on regulated rivers throughout the world to improve their ecological integrity. As a large scale disturbance, the long term sequential use of floods provides an excellent empirical approach to examine ecosystem regime shifts in rivers. This study evaluated the long term effects of floods (15 floods over eight years) on a regulated river. We hypothesized that sequential floods over time would cause a regime shift in the ecosystem. The floods resulted in little change in the physicochemistry of the river, although particulate organic carbon and particulate phosphorus were lower after the floods. The floods eliminated moss cover on bed sediments within the first year of flooding and maintained low periphyton biomass and benthic organic matter after the third year of flooding. Organic matter in transport was reduced after the third year of flooding, although peaks were still observed during rain events due to tributary inputs and side slopes. The floods reduced macroinvertebrate richness and biomass after the first year of floods, but density was not reduced until the third year. The individual mass of invertebrates decreased by about one half after the floods. Specific taxa displayed either a loss in abundance, or an increase in abundance, or an increase followed by a loss after the third year. The first three flood years were periods of nonequilibrium with coefficients of variation in all measured parameters increasing two to five times from those before the floods. Coefficients of variation decreased after the third year, although they were still higher than before the floods. Analysis of concordance using Kendall's *W* confirmed the temporal changes observed in macroinvertebrate assemblage structure. An assessment of individual flood effects showed that later floods had ~30% less effect on macroinvertebrates than early floods of similar magnitude, suggesting that the new assemblage structure is more resilient to flood disturbance. We conclude that the floods caused an ecosystem regime shift that took three years to unfold. Additional long term changes or shifts are expected as new taxa colonize the river from other sources.

Key words: ecosystem regime shift; experimental flooding; flood disturbance, resilience or resistance; macroinvertebrates; river flow regime; temporal scale.

INTRODUCTION

Flow is arguably one of the most important master variables of river ecosystems (Poff et al. 1997, Hart and Finelli 1999, Malard et al. 2006). Most aquatic organisms have evolved characteristic biological traits adapted to the natural flow regime of free flowing rivers (Lytle and Poff 2004). For example, fishes have specialized morphologies that reflect flow regimes in different types of rivers (Welcomme 1985, Poff and Allan 1995), macroinvertebrates have evolved life history traits adapted to temporary waters (Williams and Hynes 1977, Williams 1996, Stanley et al. 1997), and larger biota such as alligators and turtles have evolved life cycles in rivers that experience an annual flow pulse (Junk et al. 1989, Robinson et al. 2002).

Floods are an inherent feature of the natural flow regime of many rivers that impose strong ecological and evolutionary constraints on flowing water organisms (Poff et al. 1997). For instance, floods are important drivers in the relationship of disturbance and productivity gradients on biodiversity patterns in rivers (Biggs et al. 1999, Cardinale et al. 2006), and many benthic macroinvertebrates have evolved life cycles to account for predictable seasonal floods such as those associated with spring runoff (Robinson and Minshall 1998). The effects of single flood events, such as reductions in organism densities or standing stocks, on aquatic flora and fauna, whether predictable or unpredictable, have also been well documented (Resh et al. 1988, Boulton et al. 1992, Matthaei et al. 1997, Robinson et al. 2003). In contrast, there is a paucity of information on the ecological and evolutionary influence of experimental floods on river ecosystems (Robinson and Uehlinger 2003). Besides being excellent tests of ecological and evolutionary theory, this kind of information is espe-

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cially important with respect to regulated rivers where a paradigm shift has occurred toward incorporating a more natural flow regime in river flow management (Poff et al. 1997, Arthington et al. 2006).

The flows of most rivers of the world are regulated to some extent, with over 45 000 large dams (>15 m high) currently in operation and numerous others being built or planned for development (World Commission on Dams 2000, Nilsson et al. 2005). In addition, smaller dams outnumber large ones by orders of magnitude with potential cumulative effects on those streams and rivers (Poff and Hart 2002). The physical and biological effects of dams on downstream receiving waters have been well documented (Ward and Stanford 1979, 1995, Wallace 1990, Vinson 2001, Graf 2006), and recent efforts are beginning to document major impacts to upstream ecosystems as well (Pringle 1997, Greathouse et al. 2006). Many large dams are built to store water for electrical production, often causing reduced and constant flows in downstream waters with subsequent habitat degradation (Graf 2006). The reduction in disturbance frequency theoretically and empirically results in the loss of biodiversity and a shift toward larger competitively superior taxa (Cardinale et al. 2005, 2006). For example, in a regulated alpine river the benthic macroinvertebrate community was dominated by the large amphipod *Gammarus fossarum* with densities reaching >10 000 individuals/m² and the major food resource for brown trout (*Salmo trutta*), the sole fish species in the river (Ortlepp and Mürle 2003, Robinson et al. 2003). Although based on a long history of ecological and evolutionary constructs (e.g., Connell 1978, Huston 1979, Southwood 1988), there is growing recognition that a multivariate habitat template best explains biodiversity patterns of ecosystems (Cardinale et al. 2006), and flowing waters in particular, which should be incorporated into their management.

How ecosystems respond to environmental change such as changes in disturbance regime is a paramount question in ecology today. Current models suggest that ecosystems can respond rapidly to such changes, causing catastrophic regime shifts (Scheffer et al. 2001) or ecosystem switching to an alternative state (Lewontin 1969, Schröder et al. 2005). Three types of regime shifts are recognized and include smooth, abrupt, and discontinuous shifts in response to changes in environmental conditions through positive feedback mechanisms (Collie et al. 2004, Suding et al. 2004). The ecological resistance of the ecosystem is a primary controller of the type, if any, of regime shift (Holling 1973, Grunderson 2000). Additional knowledge is needed to accurately assess whether an ecological threshold has been crossed and the mechanisms underlying such behaviors during a regime shift (Suding et al. 2004, Groffman et al. 2006). For instance, recent evidence suggests that ecosystems experience increased variance during the transition between alternative states or regime shift (Carpenter and Brock 2006). Such

information is critical for resource managers, as the ecosystem consequences of decisions may be irreversible (Groffman et al. 2006). Most empirical evidence for regime shifts comes from studies on deserts (Kassas 1995), marine ecosystems (Van de Koppel et al. 2001, Knowlton 2004), and shallow lakes (Scheffer et al. 1993), with generally little information on flowing water systems. This type of knowledge is especially important for regulated rivers as changes in environmental conditions will likely result in some form of hysteresis (Scheffer et al. 2001) due to the loss of biodiversity following flow regulation. For example, once in a new state the system may require more than restoration of former environmental conditions to return to the former biotic state.

Study objectives and predictions

The primary goal of this study was to test whether implementing a novel disturbance regime through experimental floods would cause a regime shift in ecosystem properties of a flow regulated river, where the flow regime has been relatively constant for over 30 years. We predicted that ecosystem properties would change in response to the new habitat template of the river that resulted from a more variable flow regime. We evaluated this prediction by testing different population, community, and ecosystem level hypotheses. We expected the floods to have little effect on the physicochemistry of the river because the water source (i.e., hypolimnetic release from the dam) would be the same as before the floods. We hypothesized that the floods would reduce standing stocks of primary producers and eliminate attached moss on bed sediments. The floods should scour bed sediments and dislodge the moss within the first or second year. The pre flood stream bed was highly armored and the floods should reduce armoring and increase the porosity of bed sediments. Although the study river is nutrient rich, the floods should maintain low periphyton biomass by scouring filamentous algae from bed sediments. We hypothesized that the experimental floods would reduce benthic and transported organic matter in the river. Benthic organic matter should decrease because the bed sediments would be mobilized by the floods and benthic particulates would be flushed from the system. Seston (particulate organic matter) levels should decrease because the floods would reduce standing stocks of benthic organic matter and periphyton that are the primary instream sources of seston.

We predicted that the floods would reduce benthic macroinvertebrate density, biomass, and taxon richness, and result in higher proportions of smaller sized organisms. We hypothesized that disturbance prone taxa such as large bodied sessile taxa (e.g., *Gammarus fossarum*) would decrease in abundance and disturbance resistant taxa such as small bodied, highly mobile taxa (e.g., *Baetis* sp.) would increase in abundance from the floods. The shift in organism size was expected

because larger organisms are more associated with taxa that inhabit relatively stable flowing systems, such as before the floods. These taxa should be replaced by more disturbance resistant taxa that tend to be smaller in size.

Lastly, we hypothesized that measured properties would initially become more variable and then less variable as the ecosystem regime shift occurred. The regime shift should be observed by a change in mean values, along with an increase in variation (as coefficients of variation, CV) during the shift (Sheffer et al. 2001, Carpenter and Brock 2006). We expected the variation to decrease after the shift, although it would still be higher than before the shift because of the immediate flood effects that cause reductions in organism density and biomass. The regime shift would be related to the changes in the composition of benthic macroinvertebrates, as referred to previously. We also predicted that initial floods would have a greater impact than later floods of similar magnitude because of the regime shift in ecosystem properties and changes in macroinvertebrate composition.

Site description and flood program

The study was conducted on the Spöl River downstream of Livigno reservoir on the Swiss-Italian border (10°11'22" E, 46°36'38" N), lying within the central part of the inner Alps. The climate is continental, with relatively low precipitation and high seasonal variation in temperature (Barry 1992). Terrestrial vegetation is dominated by coniferous forest (*Picea excelsa* and *Pinus mugo*), and alder (*Alnus incana*) is common along the river margin. The river below the dam (Punt dal Gall) flows through a canyon confined valley within the Swiss National Park for ~5.7 km before entering Ova Spin reservoir. Maximum elevation of the Spöl catchment is 3302 m above sea level and the study reach was at 1660 m a.s.l. ~2.3 km downstream of Punt dal Gall. The Spöl eventually flows into the Inn River, a major tributary of the Danube. Before regulation, the Spöl had a typical flow regime dominated by snow melt/glacial melt with high flows in summer and low flows in winter (Fig. 1). Periodic peak flows or floods from heavy rainfall, between 20 m³/s and 60 m³/s, mostly occurred during the summer and into early autumn.

The Spöl is part of a complex hydroelectric scheme (Scheurer and Molinari 2003). Punt dal Gall dam became operational in 1970 and flow regulation resulted in the annual mean discharge in the Spöl to decrease from 8.6 to 1.0 m³/s. Regulated flows averaged 0.55 m³/s in winter and from 1.0 m³/s at night to 2.5 m³/s during the day in summer using hypolimnetic water from the reservoir (Fig. 1). This residual flow lacked the power to entrain and transport coarse sediments and allowed the riverbed to be clogged with fine sediments, which 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 stable flows also resulted in

dense algal mats, extensive moss beds, and an invertebrate community atypical of an alpine mountain river (Robinson et al. 2003).

The power company, the Swiss National Park, and state authorities agreed in 1996 to study the possibility of improving habitat conditions in the river by using experimental floods (Scheurer and Molinari 2003). The floods were cost neutral because of the configuration of reservoirs, aqueducts, and power houses that allowed reallocation of water for power production while maintaining residual flows in the Spöl. Residual flows were further reduced (0.55 m³/s winter, 1.45 m³/s summer) beginning in 1999 to compensate for water released during each flood (Uehlinger et al. 2003). The experimental flood program began in summer 2000, and based on the ecological results to date has been adopted in the regulatory framework of the reservoir (P. Molinari, *personal communication*).

Fifteen separate floods were released between 2000 and end of 2006 (Fig. 1). The flood program began with three floods each in 2000 and 2001, then alternating between two floods and a single flood per year since 2002. The three floods in 2000 and 2001 consisted of two smaller flows between 12 m³/s and 16 m³/s in June and August that bounded a higher flow (42 and 55 m³/s, respectively) in July. One unplanned flood in October 2000 resulted from heavy precipitation that filled the reservoir above storage capacity and caused a three day release of surplus water that peaked at 28 m³/s. After 2002, the June flood was eliminated, and a high flow occurred in July with a smaller flow in August (2002: 51.1 and 13.9 m³/s; 2004: 35.9 and 28.2 m³/s; 2006: 41.1 and 26.4 m³/s, respectively). Single floods were implemented in 2003 (41.5 m³/s) and 2005 (11.2 m³/s). Although floods <15.0 m³/s were found to be morphologically ineffective after 2001, flood flows still varied in size due to water availability between years (e.g., the small flood in 2005). Most later floods were designed to be between ~30 m³/s and 50 m³/s (Scheurer and Molinari 2003). Each flood lasted 6–8 hours with the step like rising and falling limb being constrained by the engineering mechanics of the release valve.

METHODS

A 200 m long reach ~2.3 km downstream of the dam was used during the eight years of the study. The study reach was accessed via a national park trail. Discharge was recorded at the gauging station at the dam by the Federal Office of Hydrology and Geology. A temperature logger (Minilog, Vemco, Nova Scotia, Canada) was installed at the study site and recorded temperature at 1 h intervals. The logger was downloaded every 4–6 months. The study reach was visited 72 times between 1999 and 2006 for collection of samples. Many of these visits were intentionally made 1–3 days before and 1–2 days after a particular flood, especially in the first three years of the flood program. The sampling frequency was less in the last four years of the study, although samples

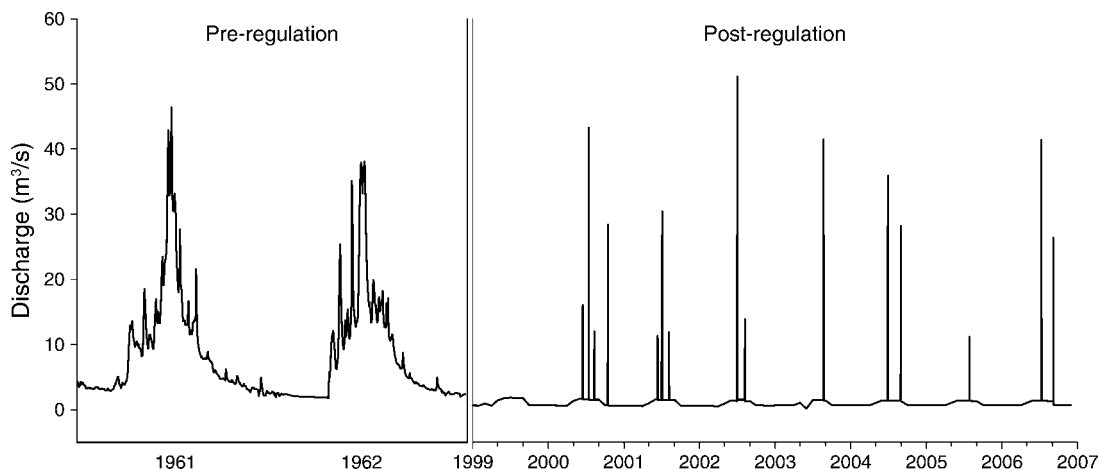


FIG. 1. The flow regime of the Spöl River (on the Swiss-Italian border) for two representative years before regulation, the year before the flood program (1999) showing the typical seasonal regulated flow, and the flow after the flood program, including each of the experimental floods. Data for 1999 and the years before regulation are daily values. Data are instantaneous values after 2000.

were still collected within five days before and after each flood. On each sampling visit, a 1 L water sample was collected from the thalweg in a polypropylene bottle for analysis of ammonium N, nitrite N, nitrate N, dissolved and particulate N, soluble reactive P, total dissolved P, particulate P, dissolved organic carbon, and particulate organic carbon following methods detailed in Tockner et al. (1997). In the field, we also measured turbidity (nephelometric turbidity units [NTU]; Cosmos, Züllig AG, Switzerland) and conductivity ($\mu\text{S}/\text{cm}$ at 20°C ; WTW LF340, Weilheim, Germany) with portable meters.

Periphyton was measured by collecting 10 rocks (cobble size) randomly within the study reach on each visit. The rocks were placed in plastic bags, returned to the laboratory, frozen at 20°C , and processed within three weeks after collection. Periphyton was removed from each rock by scrubbing with a wire brush into a bucket with water, and the dimensions (a , b , and c axes) of each rock were measured with a caliper. Aliquots of the periphyton suspension were filtered through glass fiber filters (Whatman GF/F, pre ashed at 450°C) for determination of chlorophyll a and ash free dry mass (AFDM). Chlorophyll a was determined by HPLC after extraction with hot ethanol (Meysn et al. 1994). AFDM of each sample was determined by drying the filter at 60°C , weighing, burning the filter at 500°C for 4 h, and then reweighing. Area values of chlorophyll a and AFDM were calculated as described in Uehlinger (1991). Prolific growths of moss covered many rocks in the first 2–3 years of the study and were removed by knife from each rock and biomass estimated as AFDM. Moss data were treated separately from the periphyton data in subsequent analyses.

Replicate seston samples ($N = 4$) were collected on each visit from the thalweg using a 1 m long net (100 μm mesh, aperture 11 cm). Seston refers to the organic matter suspended and transported in the water column,

excluding drifting macroinvertebrates. Water flowing through the sampler was measured with a velocity meter (MiniAir II, Schiltknecht, Switzerland) and used to calculate the volume of water filtered. Nets were deployed for 3–5 min depending on clogging. Each sample was stored in a Whirl Pak bag (Nasco, Fort Atkinson, Wisconsin, USA), frozen at 20°C , and processed within three weeks of collection. In the laboratory, each sample was filtered (Whatman GF/F, pre ashed at 450°C), all macroinvertebrates removed from the filter, and the filter then cut in half. One half of the filter was used for chlorophyll a analysis and the other half for AFDM as previously described.

Benthic macroinvertebrates were collected from riffle/run habitats on each visit ($N = 3$) using a Hess sampler (0.045 m^2 , 250 μm mesh). Riffle/run habitats are the most common habitat types in the river because it flows through a canyon confined valley. Samples were stored in plastic bottles and preserved in the field with 70% ethanol. Macroinvertebrates were hand picked from each sample using a dissecting microscope at $10\times$ magnification, identified to lowest practical taxonomic unit (usually genus), and counted. The biomass of each taxonomic group in a sample was determined by drying at 60°C and weighing. The material remaining in each benthic sample was dried at 60°C , weighed, burned at 500°C , and reweighed to obtain estimates of benthic organic matter as AFDM.

Data analysis

Water chemistry and temperature. We hypothesized that the flood program would not affect the water chemistry or temperature regime in the Spöl River. We tested this hypothesis by comparing values of measured parameters before and after the flood program began using a paired t test (Zar 1984). We also tested this hypothesis by comparing coefficients of variation (CV)

in measured values before and after the flood program began.

Periphyton, benthic, and transported organic matter.

We hypothesized that the floods would eliminate moss coverage and reduce periphyton standing crops and the quantity of seston in the Spöl. We tested this hypothesis using repeated measures ANOVA on log transformed data (Zar 1984). Post hoc testing was done with Tukey's hsd test.

Benthic macroinvertebrates. We hypothesized that macroinvertebrate taxon richness, total density, total biomass, and individual biomass would decrease as a result of the floods. We tested the hypothesis using repeated measures ANOVA on log transformed data (Zar 1984). Post hoc testing was done with Tukey's hsd test. Community level responses were examined further using principal components analysis (PCA) based on the biomass and relative density data of the different taxonomic groups. Data were log transformed (biomass) or arcsine square root transformed (relative density) prior to running the PCA (varimax rotated).

Eight taxa were sufficiently abundant to test for flood effects on their densities. Three of these taxa were expected to decrease in density based on species traits that suggested poor resistance to flood disturbance: the amphipod *Gammarus fossarum*, the turbellarian *Creobia alpina*, and Trichoptera (mostly *Allogamus uncatatus* and *Rhyacophila* spp.). Five of these taxa were expected to benefit from the floods because their species traits suggested good resistance or resilience to flood disturbance: the mayfly *Baetis* spp., the stonefly *Protonemura* sp., the blackfly *Simulium* sp., chironomid midges, and a group of various small dipterans (mostly *Dicranota* sp. and empedids), excluding chironomids. The remaining taxa were grouped as "others" and were expected to decrease in density with floods. Density changes were tested using repeated measures ANOVA on log transformed data. Post hoc testing was done with Tukey's hsd test.

Regime shift in ecosystem properties. We hypothesized that ecosystem properties would experience a temporal regime shift with an intermediate period of relative nonequilibrium. Data analyzed included macroinvertebrate density, biomass, richness, and individual biomass, benthic organic matter, periphyton chlorophyll *a* and AFDM, and seston chlorophyll *a* and AFDM. Three periods of time were compared with the analysis: pre flood data, post flood data from 2000 to 2003, and post flood data from 2004 to 2006. The time periods were selected based on a graphical summary of the different data that suggested a strong transformation period in the system between 2000 and 2003. We tested this hypothesis by comparing changes between time periods using one way ANOVA on log transformed data and coefficients of variation. We further tested the hypothesis using Kendall's *W* similarity index based on the benthic macroinvertebrate assemblages between sequential years (Zar 1984). Kendall's *W* is a measure

of concordance with values ranging from 0.0 (full concordance) to 1.0 (no concordance). Here we expected communities to initially become dissimilar and then to increase in concordance between years as the regime shift was realized.

Lastly, we tested for an increase in the resistance of the system to flood disturbance by comparing the relative change in invertebrate density and biomass, and periphyton AFDM before and after small (>10 m³/s), intermediate (>25 m³/s), and large floods (>40 m³/s) in 2000 vs. those in 2005 or 2006. Here we expected the early floods, regardless of size, to cause a greater relative change in examined properties than later floods. All statistical tests were performed using Statistica 6.0 (StatSoft 2001).

RESULTS

Changes in physical and chemical characteristics

The change in flow regime caused by the experimental floods resulted in few significant changes in measured physical or chemical parameters of the surface water (Table 1). The initial floods actively scoured lateral debris flows resulting from the encroachment of scree slopes (see Mürle et al. 2003). Mean water temperature ranged between 7°C and 8°C and remained fairly constant because of the hypolimnetic release from the reservoir. Specific conductance and turbidity also remained the same, although the CV for turbidity was higher after the floods due to inputs from tributaries during rain events. This was expected as the post flood samples encompassed a longer time period than the pre flood samples and some field samples were collected on rainy days. Constituents of nitrogen slightly decreased after the flood by ~12% but remained relatively high (e.g., mean nitrate N = 244 µg/L). Phosphorus P and dissolved P concentrations remained the same after the floods, although particulate P decreased from 9.0 to 5.1 µg/L (Table 1). Dissolved organic matter was the same before and after the flood program, but particulate organic matter decreased by about one half from 1.2 mg/L before the floods to 0.5 mg/L after the floods.

Changes in organic matter resources

Moss covered most stones in the Spöl River before the flood program, with an estimated biomass (mean ± SD) of 137 ± 286 g AFDM/m² (Uehlinger et al. 2003). By the third flood in 2000 no moss was observed on stones. The floods reduced the biomass of periphyton in the river (AFDM, $F_{1,67} = 19.09$, $P = 0.0001$; chlorophyll *a*, $F_{1,68} = 35.55$, $P = 0.0001$; Fig. 2A, B). Periphyton biomass reached maximum values between floods in 2001 and 2003 (e.g., 90 g/m² AFDM, 400–500 mg/m² chlorophyll *a*), before decreasing to relatively low values after 2004 (mean = 20 g/m² AFDM, 27 mg/m² chlorophyll *a*). Average pre flood values in 1999 were 29 g/m² AFDM and 65 mg/m² chlorophyll *a*.

The floods reduced the amount of benthic organic matter in the river ($F_{1,64} = 2.96$, $P = 0.0001$; Fig. 2C).

TABLE 1. Comparison of physical and chemical measurements and coefficient of variation (CV) recorded the year before and the years after the flood program began.

Measurements	Before flood (<i>N</i> = 9)		After flood (<i>N</i> = 63)		<i>t</i>	<i>P</i>
	Mean (SD)	CV	Mean (SD)	CV		
Temperature (°C)	7.2 (1.1)	15	7.8 (2.2)	29	0.254	0.802
Conductivity (µS/cm at 20°C)	240 (22)	9	253 (25)	10	1.451	0.179
Turbidity (NTU)†	15 (10)	67	10 (13)	127	1.250	0.244
Nitrate N (µg/L)	295 (63)	22	244 (39)	16	2.339	0.043
Dissolved N (µg/L)	384 (54)	14	336 (70)	21	2.679	0.020
Particulate N (µg/L)	28 (7)	26	22 (12)	54	2.101	0.053
Phosphorus P (µg/L)	<1 (<1)	125	<1 (<1)	115	0.109	0.916
Dissolved P (µg/L)	2.3 (2.0)	86	3.1 (3.3)	108	0.856	0.412
Particulate P (µg/L)	9.0 (4.4)	49	5.1 (5.1)	99	2.423	0.033
Dissolved organic carbon (mg/L)	0.78 (0.26)	34	0.87 (0.47)	55	0.557	0.588
Particulate organic carbon (mg/L)	1.2 (0.7)	63	0.5 (0.6)	114	3.083	0.012

Notes: Values of measured parameters were compared before and after the flood program began using a paired *t* test (Zar 1984). *P* values <0.05 are significant.

† NFU = nephelometric turbidity units.

Benthic organic matter reached pre flood levels (mean = 16.8 g/m²) between floods in 2002 and 2003 before maintaining lower levels after 2004 (mean = 4.4 g/m²). Seston levels were reduced by the floods (AFDM, $F_{1,64} = 18.27$, $P = 0.0001$; chlorophyll *a*, $F_{1,55} = 50.62$, $P = 0.0001$; Fig. 2D, E). Seston AFDM often reached high levels (>100 mg/m³) between floods probably because of particulate inputs from tributaries and side slopes during rain events (e.g., the high peaks in 2003 and 2006 were a result of intense rains in the valley). Seston chlorophyll *a*, on the other hand, peaked between floods from 2001 to 2003 (>40 mg/m³) in a similar pattern as periphyton chlorophyll *a*, before maintaining low values after 2004 (mean = 6.2 mg/m³).

Changes in macroinvertebrate assemblages

Community changes. The floods reduced the density ($F_{1,70} = 8.27$, $P = 0.0001$), biomass ($F_{1,70} = 5.41$, $P = 0.001$), taxon richness ($F_{1,70} = 2.92$, $P = 0.0001$), and individual biomass ($F_{1,70} = 1.81$, $P = 0.001$) of macroinvertebrates in the river (Fig. 3). Average density decreased from 22 700 individuals/m² in 1999 to 8800 individuals/m² after 2003. Average biomass decreased from 13.7 g/m² in 1999 to 3.2 g/m² after 2003, and richness from 12.4 taxa in 1999 to 7.1 taxa after the floods. Individual biomass decreased by about one half from 0.62 mg/individual to 0.37 mg/individual after 2003 (Fig. 2). Macroinvertebrate density typically increased between floods to pre flood values, whereas biomass usually remained below pre flood levels, probably in response to individual biomass being lower after the floods. Taxon richness decreased after the first floods in 2000 and remained low throughout the study period.

Results of the principal components analysis (PCA) based on the relative abundances of taxa showed a change in assemblage composition from 1999/2000 to 2001, another change from 2001 to 2002, and a subsequent change following 2002 (Fig. 4A). The first two axes explained 45% of the variation in the data and were loaded by *Baetis* spp. and *Protonemura* sp. along

axis 1 and *Gammarus fossarum* and chironomids along axis 2. The data suggest that the relative abundances of *G. fossarum* and chironomids decreased after 2000 and then increased again after 2003, whereas the relative abundances of *Baetis* spp. and *Protonemura* sp. increased after the floods, especially after 2002. The PCA results based on the biomass of taxa also showed that assemblage structure changed after the floods (Fig. 4B). Here the first two axes explained 52% of the variation in the data with axis 1 being loaded by *Baetis* spp., *Leuctra* sp., chironomids, and *Dicronota* sp., and axis 2 by *Crenobia alpina*, *Rhithrogena* spp., trichopteran, and Oligochaeta. The scatterplot shows a major change in structure after 2000 along axis 2 with decreases in those taxa explaining axis 2, and a gradual change in structure between years along axis 1 with increases in biomass for those taxa explaining this axis.

Population changes. The floods reduced the density of *Gammarus fossarum* in the Spöl ($F_{1,70} = 4.35$, $P = 0.0001$; Fig. 5A). Average density before the floods was 7000 individuals/m² and it decreased to 2540 individuals/m² after 2003. The floods reduced the average abundance of chironomids from 8340 individuals/m² before the floods to 2360 individuals/m² after 2003 ($F_{1,70} = 5.76$, $P = 0.0001$; Fig. 5B). The density of *Baetis* spp. increased after the floods with interflood peaks reaching >6000 individuals/m² compared to the pre flood average density of 1160 individuals/m² ($F_{1,70} = 3.41$, $P = 0.0001$; Fig. 5C). *Protonemura* sp. also benefited from the floods with average density increasing from 240 individuals/m² in 1999 to 1360 individuals/m² after the floods ($F_{1,70} = 10.75$, $P = 0.0001$; Fig. 5D).

Simulium sp. showed an initial sharp increase in density (>8000 individuals/m²) after the floods followed by a decrease after 2003 to levels observed before the floods (<100 individuals/m²; $F_{1,70} = 3.40$, $P = 0.0001$; Fig. 5E). The floods reduced the density of *Crenobia alpina* from an average 2180 individuals/m² in 1999 to 132 individuals/m² after the floods ($F_{1,70} = 3.34$, $P = 0.0001$; Fig. 5F). Trichopteran, mostly represented by

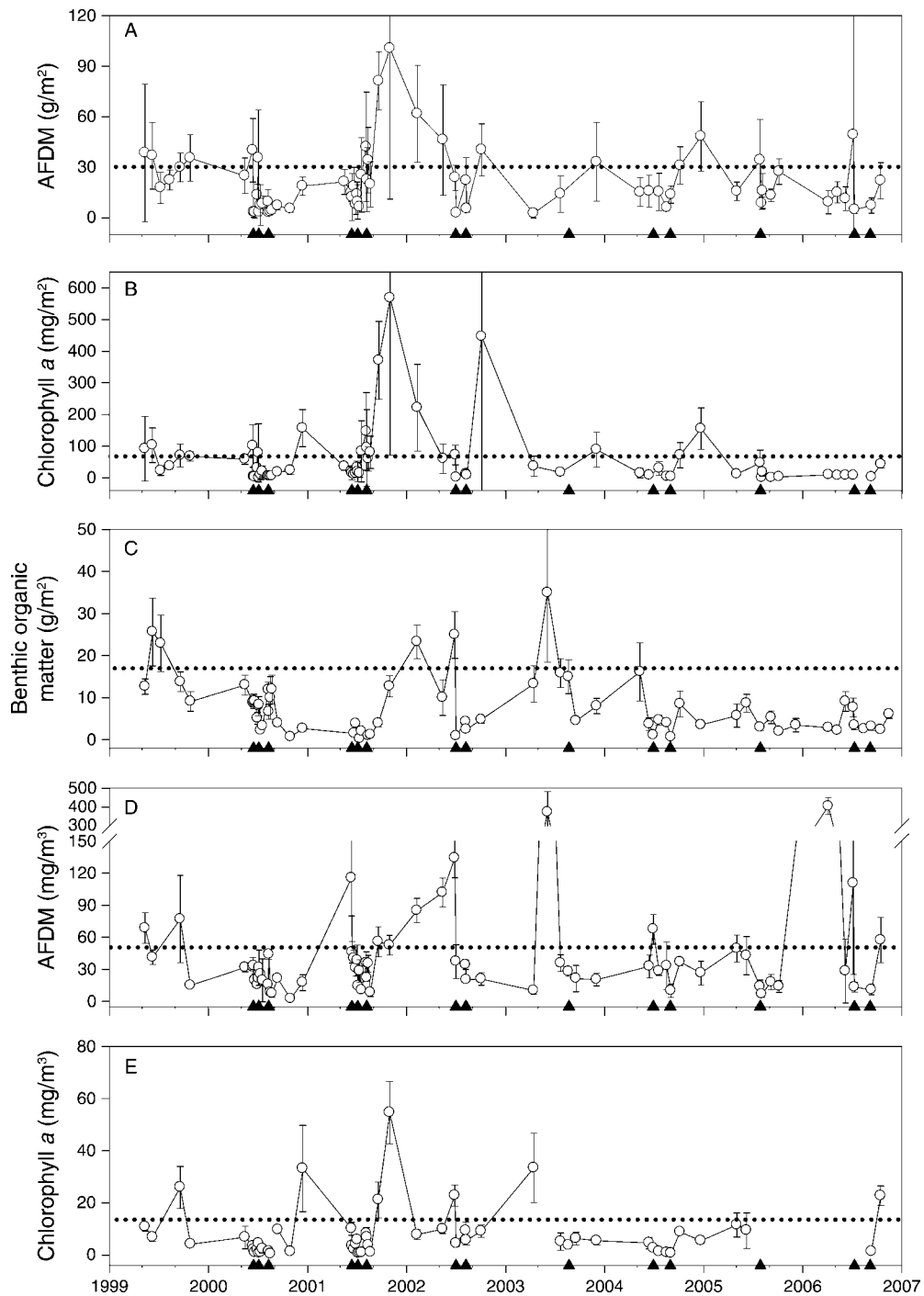


Fig. 2. Temporal changes in periphyton (A) AFDM (ash free dry mass) and (B) chlorophyll *a* ($N = 10$ for each collection date); (C) temporal changes in benthic organic matter ($N = 3$ per date); and temporal changes in seston (D) AFDM and (E) chlorophyll *a* ($N = 4$ per date). All values are means \pm SD. Solid triangles along the *x* axis of each plot show the date of each flood. The dotted line represents the mean value for samples collected the year before the flood program.

Allogamus uncatius and *Rhyacophila* spp., showed an autumn peak in the pre flood year that was not present after the floods, and densities remained low but relatively constant after the floods ($F_{1,70} = 7.51$, $P = 0.0001$; Fig. 5G). Other Diptera, mostly *Dicranota* sp.

and empedids, showed interflood peaks in density of >300 individuals/ m^2 that were not evident in 1999 when average density was 100 individuals/ m^2 ($F_{1,70} = 5.74$, $P = 0.0001$; Fig. 5H). The group labeled as “others” showed an initial increase in density after the floods due to a

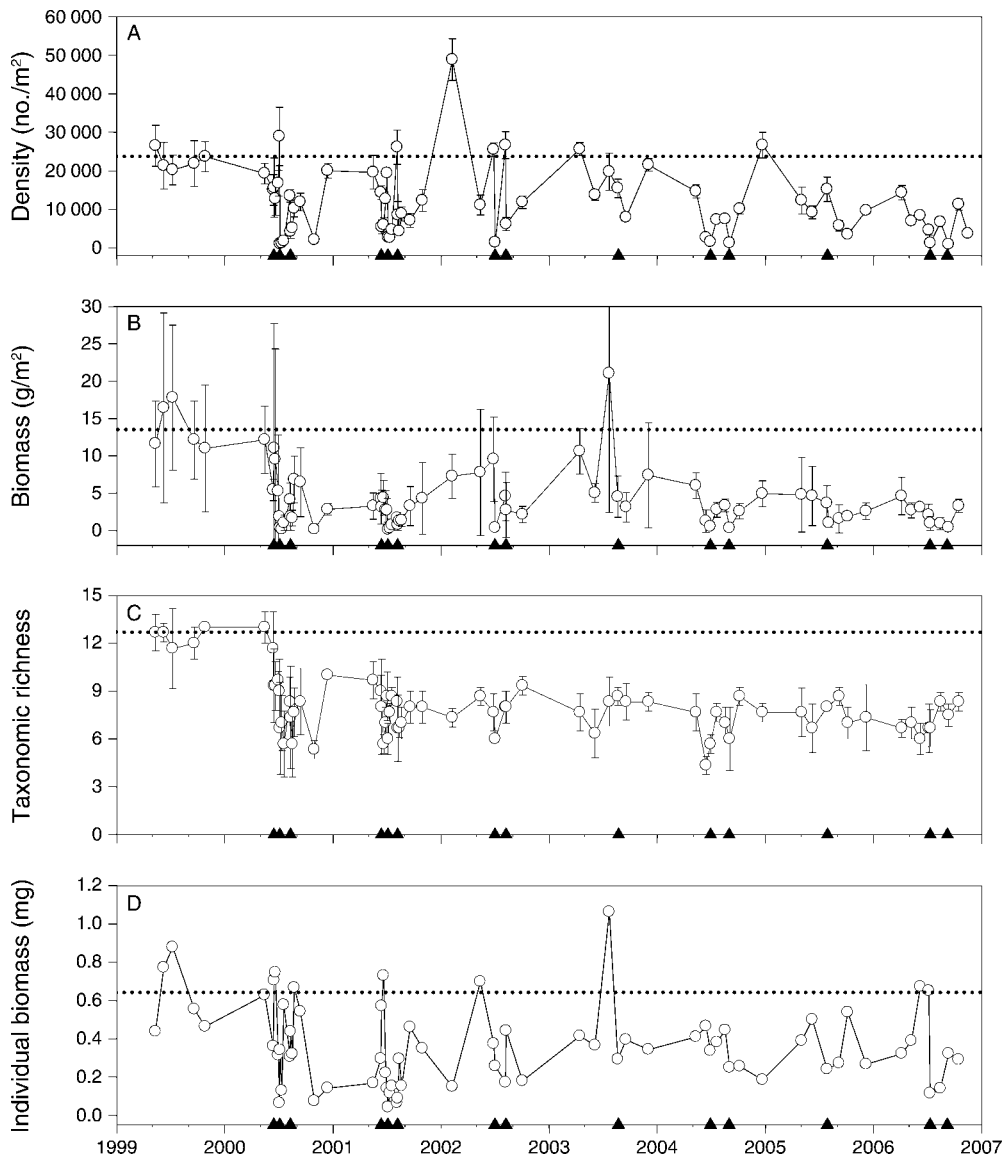


FIG. 3. Temporal changes in macroinvertebrate (A) density, (B) biomass, (C) taxonomic richness, and (D) individual biomass. All values are means \pm SD; $N = 3$ per date. Solid triangles along the x axis of each plot show the date of each flood. The dotted line represents the mean value of samples collected the year before the flood program.

peak in the density of *Leuctra* sp. in 2000–2001 (>6000 individuals/m²), followed by a decrease to an average 40 individuals/m² after 2002 ($F_{1,70} = 5.74$, $P = 0.0001$; Fig. 5I).

Regime shift in ecosystem properties

Comparison of ecosystem properties before the flood (“Before”) with those between 2000 and 2003 (“Post 1”) and those between 2004 and 2006 (“Post 2”) showed a decrease in macroinvertebrate density ($F_{1,2} = 7.77$, $P = 0.001$), biomass ($F_{1,2} = 26.09$, $P = 0.0001$), taxon richness ($F_{1,2} = 41.79$, $P = 0.0001$), and individual biomass ($F_{1,2} = 5.03$, $P = 0.007$; Fig. 6A–D). Tukey’s test showed that Before was higher than Post 1 and Post 2 ($P < 0.05$),

but Post 1 and Post 2 were not different ($P > 0.05$) for these four measures. Comparison also showed that benthic organic matter decreased between periods ($F_{1,2} = 13.71$, $P = 0.0001$; Fig. 6E) with Tukey’s test indicating that Before was higher than Post 1 and Post 2 ($P < 0.05$), but Post 1 and Post 2 were not different ($P > 0.05$). Periphyton biomass also decreased after the floods (chlorophyll *a*, $F_{1,2} = 40.98$, $P = 0.0001$; AFDM, $F_{1,2} = 24.48$, $P = 0.0001$; Fig. 6F, G), with Tukey’s test indicating that Before and Post 1 were higher than Post 2 for chlorophyll *a* ($P < 0.05$) and Before was higher than Post 1 and Post 2 for AFDM ($P < 0.05$). Seston AFDM did not differ among periods ($F_{1,2} = 2.65$, $P = 0.072$), whereas seston chlorophyll *a* decreased after the floods

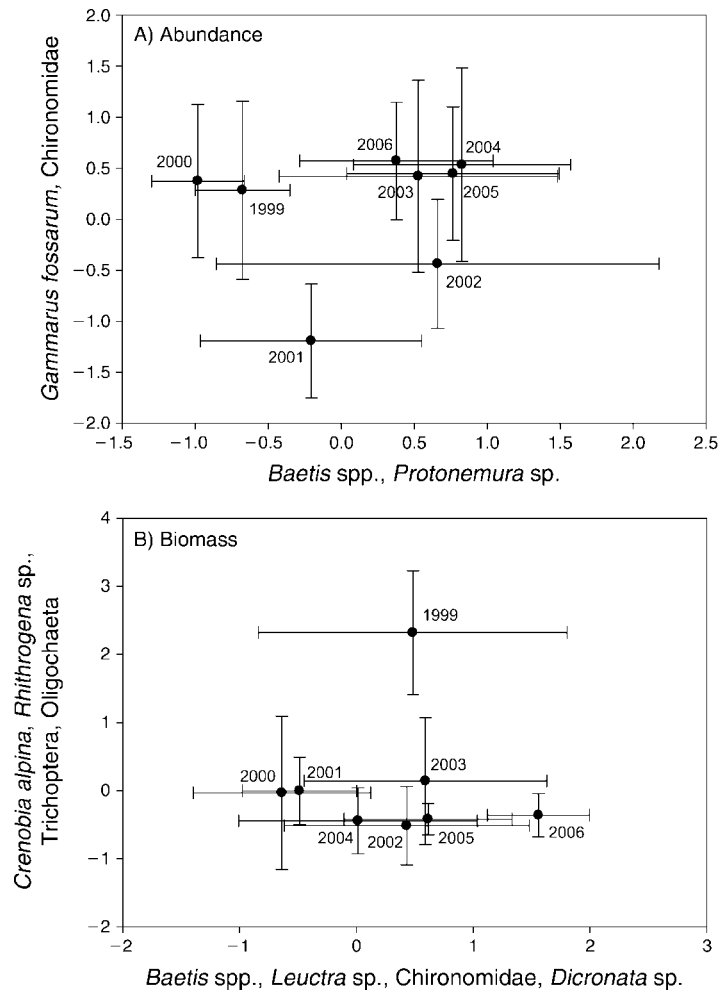


FIG. 4. Scatterplot of the results from the principal components analysis based on (A) the relative abundance of taxa and (B) the biomass of taxa. Symbols show means \pm SD of factor scores for samples collected each year of the study along the two primary axes. Taxa labeling each axis had factor loads of 0.70 or higher for that axis.

($F_{1,2} = 2.97$, $P = 0.05$; Fig. 6H, I). Tukey's test showed that seston biomass (AFDM and chlorophyll *a*) of Post 2 samples was lower than that of Before samples ($P < 0.05$), and Post 1 samples were intermediate to Before and Post 2 ($P > 0.05$).

In all comparisons, the coefficient of variation (CV) increased two to five times from the Before period to the Post 1 period (Fig. 6A I, solid bars). The CV then decreased for seven of the nine measures from the Post 1 period to Post 2 period. Sample CVs remained similar between Post 1 and Post 2 for macroinvertebrate density and taxon richness. For five of nine measures, the Post 2 sample CV was intermediate to the Before and Post 1 CVs. Before and Post 2 CVs were similar for individual biomass and seston chlorophyll *a*.

Kendall's W revealed changes in macroinvertebrate assemblage structure between different years of the study even though taxon richness was relatively low overall. This metric showed a major shift in assemblage structure between 1999 and 2000 ($W = 0.236$, $P < 0.05$; Table 2). The metric then indicated that a similar assemblage structure was present from 2000 through 2002 ($W = 0.001$, $P > 0.05$), followed by a shift between

2003 and 2004 ($W = 0.063$, $P < 0.05$). Assemblage structure then was similar between 2004 and 2006 with $W = 0.007$ ($P > 0.05$) and 0.015 ($P > 0.05$), respectively. The percentage change in invertebrate biomass and density after later large floods was lower (usually $>30\%$ less) than the change from earlier floods (Fig. 7). Small floods (>10 m³/s) had similar low effects on invertebrate biomass and density regardless of when they occurred. Small later floods (>10 m³/s) had less of an effect on periphyton AFDM, but large floods (>40 m³/s) had similar effects on periphyton biomass regardless of when they occurred.

DISCUSSION

Changes in physicochemistry

We predicted few changes in the physicochemistry of the surface water in the Spöil River because the source of water was the same (i.e., hypolimnetic reservoir water), regardless of the floods. This kind of release maintained water temperatures and nutrient concentrations similar to those before the floods. The most significant physical change was obviously the altered flow regime that

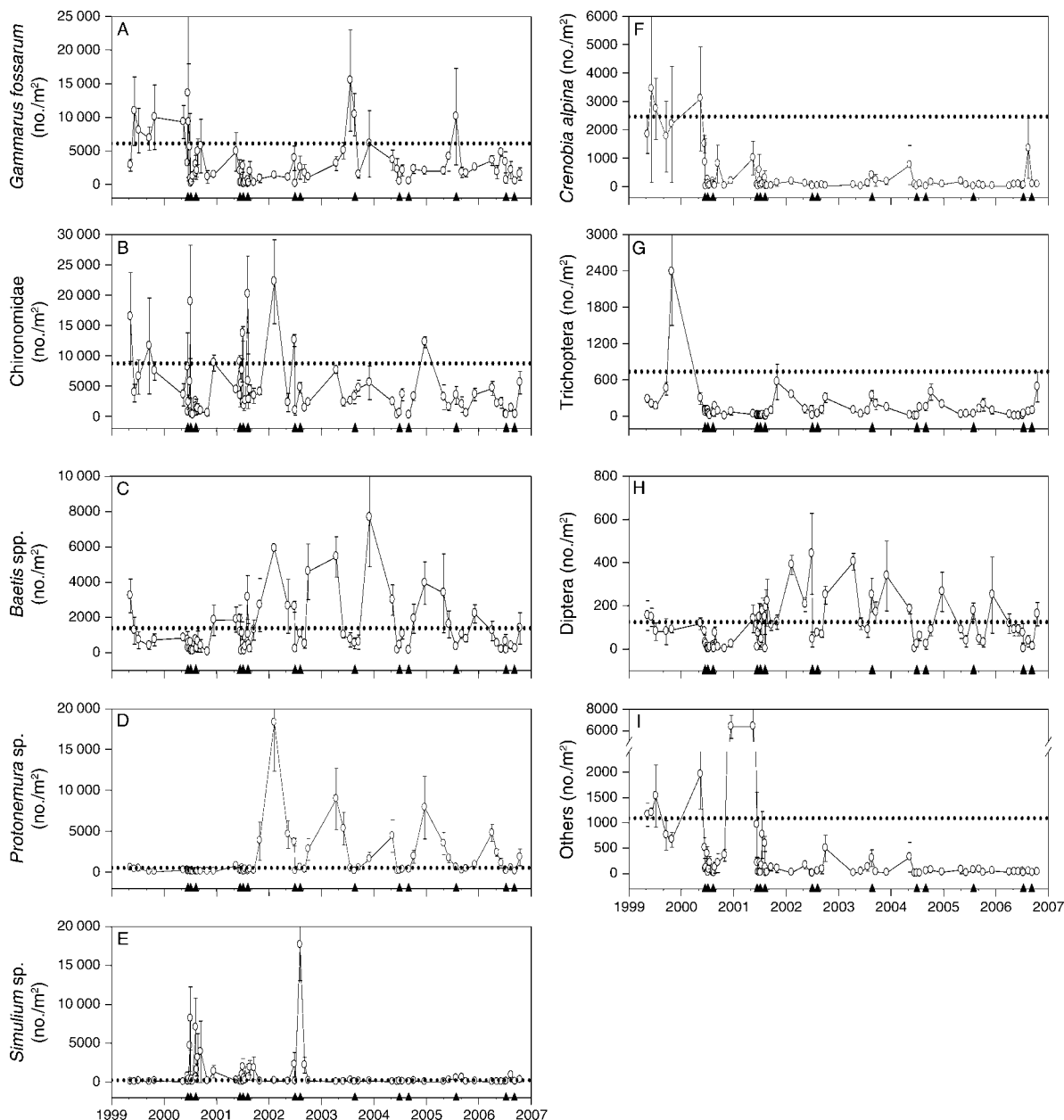


FIG. 5. Temporal changes in density (mean \pm SD) of (A) *Gammarus fossarum*, (B) Chironomidae, (C) *Baetis* spp., (D) *Protonemura* sp., (E) *Simulium* sp., (F) *Crenobia alpina*, (G) Trichoptera, (H) Diptera other than chironomids, and (I) all other taxa combined. $N = 3$ for each collection date. Solid triangles along the x axis of each plot show the date of each flood. The dotted line represents the mean value of samples collected the year before the flood program.

incorporated floods of various magnitudes (Fig. 1). In contrast to restoring the natural flow regime (sensu Poff et al. 1997), flows between each flood were regulated as before the floods and represented a compromise between economy and ecology (Scheurer and Molinari 2003). For instance, the natural high flows that would occur in summer from glacial melt and rain events were not present during the flood program. The flood peaks during the flood program were similar to flood peaks before regulation, although the duration was shorter

because the amount of water available for use during each flood was regulated by the power authorities.

A result of earlier research suggested the smaller floods ($10\text{--}15\text{ m}^3/\text{s}$) that were effective in mobilizing bed sediments in the first year had lost that ability in later years (Mürle et al. 2003). Part of this result was due to the reduction of fine sediments that could be mobilized by small floods. The fine sediments were effectively flushed from the system with the earlier floods and, as a consequence, larger floods were needed later to mobilize

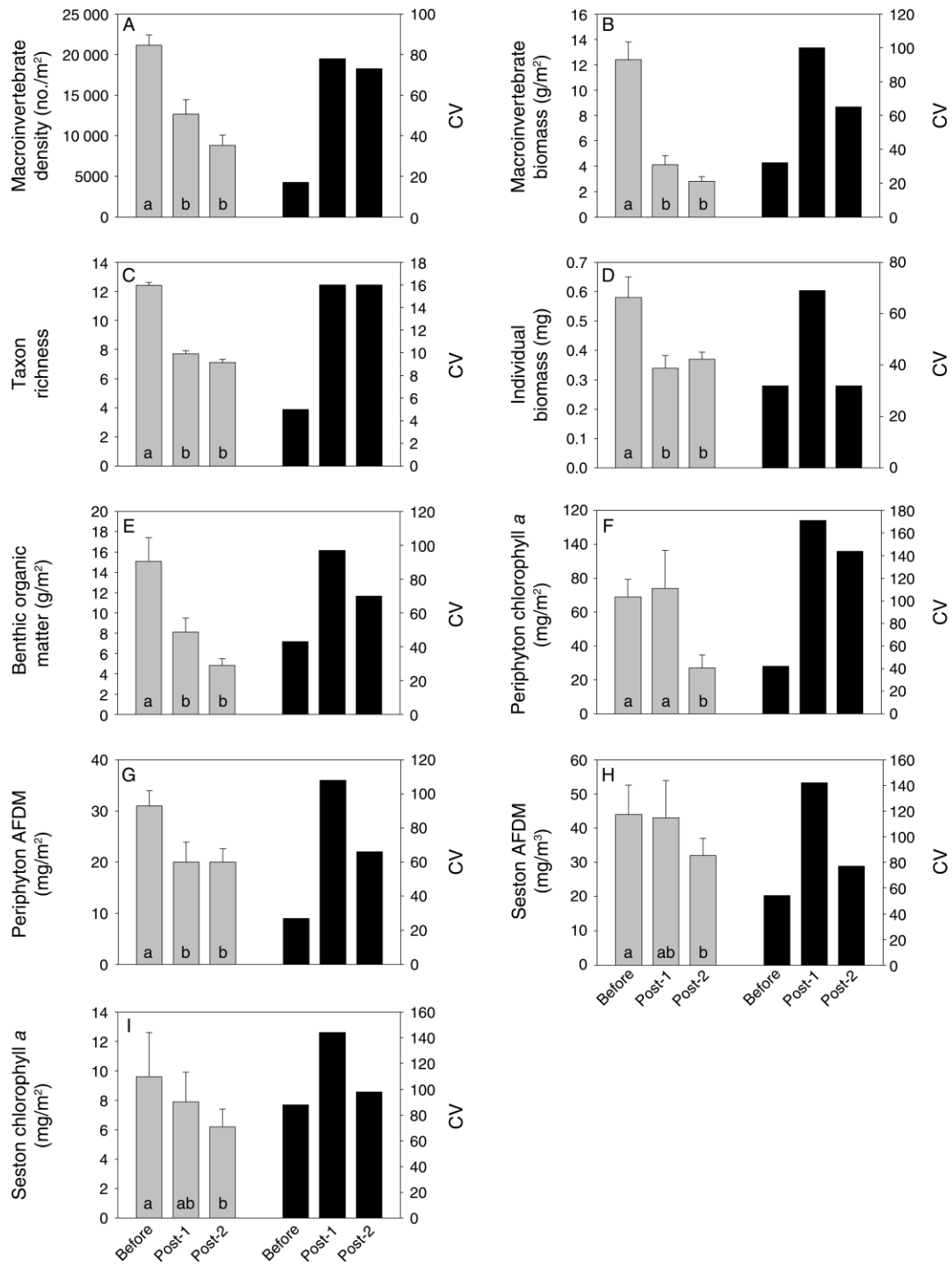


FIG. 6. Gray bars (means + SD) and black bars (coefficients of variation) for samples collected before the floods, samples collected after the first flood in 2000 and until just before the flood in 2003 (Post 1), and samples collected after the flood of 2003 (Post 2). Data are presented for (A) macroinvertebrate density, (B) macroinvertebrate biomass, (C) taxon richness, (D) individual biomass, (E) benthic organic matter, (F) periphyton chlorophyll *a*, (G) periphyton AFDM, (H) seston AFDM, and (I) seston chlorophyll *a*. Letters within bars indicate significant differences at $P < 0.05$ based on Tukey's post hoc test.

TABLE 2. Results of community similarity analysis between years using Kendall's W based on taxa densities.

Year	1999	2000	2001	2002	2003	2004	2005	2006
1999	0.000	0.236	0.005	0.056	0.061	0.094	0.043	0.120
2000		0.000	0.001	0.001	0.011	0.071	0.057	0.018
2001			0.000	0.031	0.034	0.031	0.047	0.047
2002				0.000	0.025	0.023	0.073	0.051
2003					0.000	0.063	0.090	0.007
2004						0.000	0.007	0.015
2005							0.000	0.007
2006								0.000

Note: Values range from 0.0 to 1.0, with identical assemblages having values of 0.0 and assemblages that differ completely having values of 1.0.

the larger sediments that presently dominate the stream bed. The observed decrease in particulate organic matter and particulate P after the floods may be related to this flushing of fine sediments. A primary management objective of the flood program was to increase the porosity of bed sediments to improve the reproductive potential of the fishery, as the bed was heavily armored before the floods (Uehlinger et al. 2003). This objective was met with a continuous increase in the number of redds being documented each year after the floods (Ortlepp and Mürle 2003). Lastly, scree slopes along the Spöl continuously add larger substrate and minimize any loss in habitat resulting from sediment deficits.

Changes in organic matter resources

The floods reduced organic matter resources in the river as predicted. The mobilization of bed sediments caused the loss of attached moss within the first year and shifted primary production to that of diatoms and periodic growths of filamentous algae. Algal standing stocks reached extremely high levels (>400 mg/m²

chlorophyll *a*) between floods in the second and third year of the program before maintaining levels after 2003 at two times below average levels before the floods. The floods also caused a fourfold decrease in benthic organic matter, but not until after the third year of the flood program. As expected, each individual flood reduced the standing stocks of algae and benthic organic matter, and those short term dynamics have been documented in a number of other studies (Fisher et al. 1982, Grimm and Fisher 1989, Uehlinger et al. 1996). The results of this study indicate that the long term use of multiple annual floods can maintain low organic matter resources in flow regulated rivers. High organic loads in flow regulated rivers facilitate the armoring and clogging of bed sediments and reduce the habitat availability for invertebrates and fish.

The change in organic matter resources is associated with changes in food resource quantity and quality and habitat conditions that ultimately affect and cascade through the aquatic food web and potentially into the adjacent terrestrial landscape. A decrease in food resource quantity can limit organism abundances, and changes in quality and habitat can influence the kinds of organisms present and the life history of those organisms. For instance, the reduction in gammarid abundance may be related to the loss of moss habitat in the river that provided refuge from foraging fish and trapped organic particles for food. Rader et al. (2007) also noted the importance of moss as a habitat for particular macroinvertebrates in the flow regulated section of the Colorado River (also see Englund 1991). Last, emerging insects from rivers often subsidize terrestrial organisms such as carabid beetles and spiders along shorelines (Nakano and Murakami 2001, Paetzhold et al. 2005) and birds and bats that forage along river corridors (Power and Dietrich 2002, Power

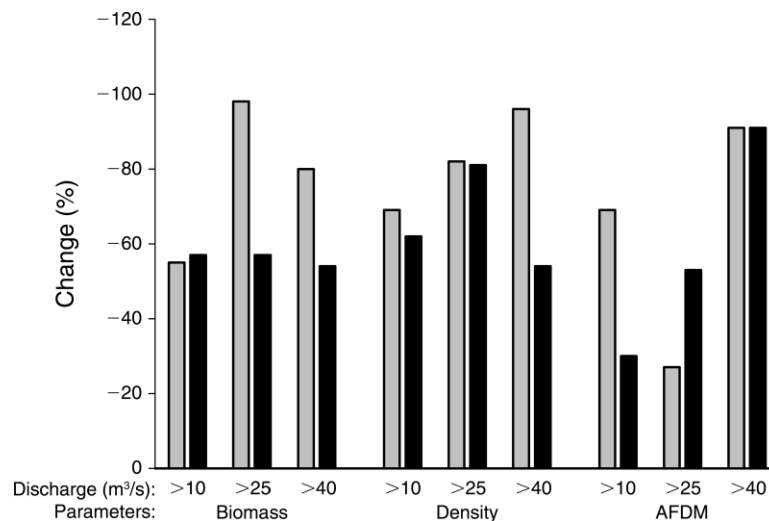


FIG. 7. The percentage change (relative decrease) in invertebrate biomass and density and in periphyton AFDM immediately following floods of different magnitude (>10 , >25 , and >40 m³/s) in the first and second year (2000 and 2001) of the flood program (gray bars) relative to floods of similar magnitude after 2004 (black bars).

et al. 2004). Indeed, secondary producers in rivers that emerge as terrestrial adults can significantly influence the abundance and distribution patterns of terrestrial organisms in riparian areas (Nakano and Murakami 2001).

Seston chlorophyll *a* showed temporal patterns similar to that of periphyton chlorophyll *a*, suggesting that the algal component of seston originated from the sloughing of benthic algae. In contrast, seston AFDM had extremely high values on some collection days that were unrelated to benthic algal standing crops or benthic organic matter. These peaks always occurred on collection days when it rained, suggesting that the seston organic matter was derived from adjacent side slopes and inputs from tributaries. A common effect of dams on downstream waters is the reduction of upstream particulates that are deposited in the reservoir (Ward and Stanford 1979). These data suggest that tributaries could be important sources of particulate organic matter in flow managed rivers, potentially subsidizing organic matter resources in these rivers between floods. This organic matter may contribute to the overall productivity of the system that would otherwise be reduced because of frequent flooding. As such, tributaries can mitigate the energetic losses associated with the reduced organic matter inputs from upstream sources. Tributaries have been found to be important modifiers of ecosystem dynamics in natural flowing waters via inputs of organic matter and drifting invertebrates (Kiffney et al. 2006), and should be considered in management schemes of regulated rivers.

Changes in benthic macroinvertebrates

The data support our hypothesis of a flood caused reduction in macroinvertebrate richness, biomass, and density. Taxonomic richness decreased by about five taxa in the first year of the flood program and has not subsequently increased. Flow regulation below dams typically results in a loss of biodiversity as the system becomes dominated by a few highly abundant taxa (Vinson 2001). This pattern was evident in the Spöl with large bodied gammarids dominating macroinvertebrate assemblages. Most of the common taxa remained in the system after the floods and the lower richness was due to a loss of less common or rare taxa. Rader et al. (2007) also attributed the lower richness in the years after a major flood in a regulated river to the loss of rare taxa. Single floods typically reduce taxonomic richness in streams immediately following floods with richness quickly recovering to pre flood levels in a matter of weeks (Resh et al. 1988, Robinson et al. 2003). Our results suggest that the long term use of multiple floods can limit the distribution and abundance of some taxa, thereby allowing other taxa to maintain populations even though overall richness values may be reduced. We would expect richness to increase again as more taxa colonize the river from other sources, but this clearly requires a long term multidecadal perspective. The

colonization of the river by additional taxa may also be limited by the temperature regime in the river that was unchanged by the flood program. Temperature and its regime can have a major influence on macroinvertebrate life histories (Hynes 1970, Vannote and Sweeney 1980).

The floods maintained low macroinvertebrate biomass and density in the river reach. Biomass decreased fourfold and density threefold, resulting from the sharp decrease in the density of large bodied organisms, gammarids in particular. Indeed, the average individual size of organisms decreased by almost one half after the flood program. The density of organisms recovered quickly between floods, but these were mostly smaller short lived taxa such as baetid mayflies and protonemurid stoneflies. Baetids are well known to be highly resilient to disturbance, often being the initial colonizers of denuded substrates (Robinson and Minshall 1986). It remains to be tested whether the decrease in biomass and density translates to lower overall secondary production, or whether the decrease in large bodied organisms was offset by the increase in smaller short lived organisms. Based on literature values (Benke 1984, Robinson and Minshall 1998), annual production: biomass ratios (P:B ratios) are around 5-10 for univoltine macroinvertebrates and can be up to 200 for some multivoltine taxa such as chironomids. This order of magnitude difference in population productivity may allow the total productivity of the system to remain at a relatively similar level after the floods to that before the floods. Fish condition has remained the same after the floods (Ortlepp and Mürle 2003), suggesting that food resources are adequate for the fish.

Three different response patterns to the floods were observed, excluding the complete loss of a taxon. The first response was exhibited by the gammarids and the flatworm *Crenobia alpina*. These taxa decreased in abundance within the first year of flooding and remained at low densities throughout the following study years. The gammarids demonstrated the importance of implementing multiple floods each year as their numbers increased quickly to pre flood levels in years when only a single flood occurred (i.e., 2003 and 2005). A second type of response was shown by baetid mayflies and protonemurid stoneflies. These taxa were reduced by each flood but recovered quickly between floods. Here baetids recovered rapidly within days to weeks, whereas the protonemurids required weeks to even months to recover. The difference may be related to the mode of dispersal by the two taxa, as baetids are known to drift and protonemurids are active crawlers. Further, the life cycles may differ with baetids showing faster development and perhaps higher reproductive potential than the stonefly. The third response was demonstrated by *Simulium* blackflies and the stonefly *Leuctra* sp. These taxa increased in abundance in the first three years of the flood program and then subsequently decreased in abundance to low levels after the third year. These taxa

also showed low abundances before the floods, suggesting that they quickly capitalized on the novel habitat conditions early on but failed to maintain high population densities later. The exact mechanism for the decrease in abundance later in the flood program is unknown, but may be related to competitive interactions with other more successful taxa such as baetids and protonemurids. *Simulium* blackflies have been shown to be poor competitors with other macroinvertebrates such as caddisflies, maintaining populations by quickly recolonizing denuded substrates following disturbance (Hemphill and Cooper 1983). Our data suggest other more complex interactions are occurring over the long term. For example, the flood frequency may be suboptimal for some taxa to sustain large population sizes over the long term; such complex dynamics are missed when examining short term data sets.

Regime shift of ecosystem properties

Flow regulation below dams often causes an abrupt shift in biotic communities in response to altered habitat conditions resulting from such regulation (Graf 2006). The regulation of flow below dams causes the downstream system to pass an ecological threshold that shifts the ecosystem into a new or alternate state (*sensu* Scheffer et al. 2001). These alternate states are sustained for years as habitat conditions are maintained by flow regulation, below large dams in particular. Present research also suggests strong upstream effects of dams on stream ecosystems (Greathouse et al. 2006), although the threshold for ecosystem change may be less distinct than that observed for downstream waters. Due to the ecological consequences of flow regulation on stream ecosystems and their functioning, there has been strong emphasis in the last decade towards restoring a more natural flow regime to flow regulated rivers to improve biodiversity (*sensu* Poff et al. 1997, Arthington et al. 2006). Although economic policies obviously influence how flows are regulated within a particular river (e.g., Poff et al. 2003), how rivers respond over the long term to such changes in flow have been little documented (Robinson and Uehlinger 2003). An overriding question is whether the biodiversity of such rivers will return to pre regulated conditions or will the system enter a stage of hysteresis as observed for other ecosystems such as lakes (Scheffer et al. 2001), oceans (Knowlton 2004), or terrestrial landscapes (Anderson et al. 2000, Suding et al. 2004). The answer has important implications regarding modeling efforts on flow regime changes in different rivers, and the ecosystem consequences of such flow changes.

Our results suggest that the experimental floods caused an ecosystem regime shift in the study reach of the Spöl River. The river ecosystem passed through a three year transition period (i.e., an ecological threshold) before completely shifting into a new or alternate ecosystem state in year 4 of the flood program. The ecological threshold was measurable as an increase in

variance, here as coefficients of variation, in all measured ecosystem parameters during the transition period (Fig. 6). Carpenter and Brock (2006) suggest that an increasing variance is a good indicator of an ecosystem moving through an ecological transition. An important finding from our data is that the transition period lasted for a period of years and was not observed as an easily definable abrupt change. This has important implications for resource managers that may perceive ecological transitions to be abrupt and occur relatively rapidly. A long term perspective is necessary to fully document and understand ecosystem change, especially when drawing conclusions regarding management policies. Groffman et al. (2006) conclude that knowledge regarding ecological thresholds is imperative towards understanding and implementing management strategies.

Although the floods caused the ecosystem to shift into an alternate state, the system appears to still be in a stage of hysteresis (*sensu* Scheffer et al. 2001). Van Nes and Scheffer (2005) suggest that the temporal length of hysteresis is related to dispersion and the spatial heterogeneity of the system. The inherent high spatial heterogeneity of rivers may be one reason for the delayed multiyear response in ecosystem properties to the new flow regime. Dispersion of control variables such as flood effects on river morphology may be fast in river ecosystems, but ecological responses may be complicated by organism dispersal and colonization abilities. For instance, most changes in macroinvertebrate community structure were based on changes in taxa already present in the system. The loss of taxa following flow regulation may impede the recolonization of such taxa following a change in flow regime. Colonization would be dependent on the dispersal ability of taxa from other rivers and streams with viable populations and may take years in a landscape context. The floods clearly benefited more disturbance resistant taxa that typically inhabit rivers with more variable flows, but the loss of taxa influences the degree of reversibility or resilience displayed by the river. Such irreversibility has been documented in a number of ecosystem types and partially explains the lack of a slow recovery following perturbation (e.g., Knowlton 2004, Suding et al. 2004). We expect that a new alternate state will transpire as new taxa colonize the river from other sources, which may take a decade or more to occur.

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