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Feature Article

Effects of a multi-year experimental flood regime on macroinvertebrates downstream of a reservoir

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Abstract. We examined the response of stream macroinvertebrates to a multiple-year experimental flood regime downstream of a large reservoir. Benthic samples were collected from the River Spöl prior to the initial flood (1999) and at periodic intervals before and after eight floods from 2000 through 2002. Three artificial floods occurred each in 2000 and 2001, and two floods were implemented in 2002. We also sampled macroinvertebrates in an adjacent tributary (Val da l'Aqua) on the same dates as in the Spöl to assess the natural temporal variability in assemblage structure. The regulated baseflow discharge in the Spöl was < 2.5 m^3/s, whereas the floods ranged from 10 m^3/s to over 25 m^3/s with some flood peaks reaching > 40 m^3/s for a short period. Repeated measures ANOVA indicated that the floods significantly reduced macroinvertebrate densities in the Spöl, although recovery to pre-flood densities occurred within a matter of weeks to densities found in 1999. A principal components analysis revealed that assemblage composition shifted in response to the recurring floods, first from 1999 to 2000 and then from 2000 to 2001/2. Taxa that decreased in abundance due to the floods included the Gammaridae (*Gammarus fossarum*) and Turbellaria (*Crenobia alpina*). Taxa that increased in abundance included Baetidae, Chironomidae, and Simuliidae. Some Plecoptera, Trichoptera, and Heptageniidae that were negatively impacted by the floods in 2000, subsequently increased in abundance. Our data suggest that the response of macroinvertebrates to experimental floods occurs over a period of years rather than months, as species composition adjusts to the new and more variable habitat template. Future changes are expected as additional species begin to colonize the river from adjacent sources. The results clearly show that the experimental flood regime should be maintained if resource managers wish to sustain the development of a more natural macroinvertebrate assemblage.

Key words. Flood pulse; flow regime; stream insects; disturbance; succession.

Introduction

Flooding is a natural feature of most rivers on the face of the earth (Junk et al., 1989; Sparks et al., 1998). Indeed, the natural flow regime incorporating flood and flow pulses is now recognized as important in maintaining both habitat and biotic diversity (Junk et al., 1989; Poff et al., 1997; Tockner et al., 1999). Over the centuries humans have regulated many rivers for flood control to meet a variety of management objectives (Dynesius and Nilsson, 1994). Regulation has resulted in over 40,000 large dams (>15 m high) worldwide (Oud and Muir, 1997), with smaller dams outnumbering large ones by orders of magnitude (Poff and Hart, 2002). Although numerous smaller dams are now being removed, in the USA in particular (Babbitt, 2002), most large dams will remain in place or are being built (Pringle, 2001), especially in developing countries (e.g., Three Gorges Dam in China was

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completed in 2002; see Pearce, 2003). The physical effects of dams on downstream receiving waters is well-documented (Ward and Stanford, 1979, 1995; Wallace, 1990; Patten et al., 2001), and includes changes in temperature and flow regimes (Poff et al., 1997; Vinson, 2001) as well as losses in lateral connectivity (Benke et al., 2000). Such physical and chemical changes to the aquatic habitat can significantly alter the aquatic macroinvertebrate community (e. g., Brittain and Saltveit, 1989).

It is becoming increasingly clear that large dams will continue to dominate many of the world's river systems, and mitigation measures other than dam removal will be necessary if natural habitat conditions are to be maintained in rivers with large dams (Petts, 1996; Powell, 2002). One avenue of mitigation is restoring some semblance of the natural flow regime (Poff et al., 1997) through implementation of a flood pulse program (e. g., Middleton, 2002). Although a number of studies have examined the effects of single floods (flushing flows) on riverine ecosystems below dams (Reiser et al., 1985; Kondolf and Wilcock, 1996; Molles et al., 1998; Patten et al., 2001), we are aware of no study that examined the effects of intra-annual flood flows in multiple years (but see Robinson et al., 2003). This is not unexpected since the implementation of a flood program can be highly complex and take many years at substantial financial cost (Andrews and Pizzi, 2000). The flood regime implemented in the present study was cost-neutral, however, as no economic cost was realized from the release of water from the reservoir (Scheurer, 2000; Scheurer et al., 2003).

Flood pulses affect all aspects of riverine ecosystems, including the physico-chemical attributes of habitats, and both terrestrial and aquatic flora and fauna (Ward and Stanford, 1979; Junk et al., 1989). The objective of the present report was to document changes that occurred in the structure of macroinvertebrate assemblages in the river below a large dam/reservoir in relation to intra-annual floods over a 4-year period. Readers should refer to other articles in this series for the effects of the experimental floods on changes in instream habitat, fishes, and periphyton. It is important to recognize that different groups of organisms respond at different temporal trajectories that reflect the variety of life histories and generation times of the various populations of study.

Materials and methods

Description of study sites

The study was conducted in the Swiss National Park on the River Spöl, which flows from the Livigno Reservoir in Italy (Fig. 1); the reservoir dam (Punt dal Gall) sits on

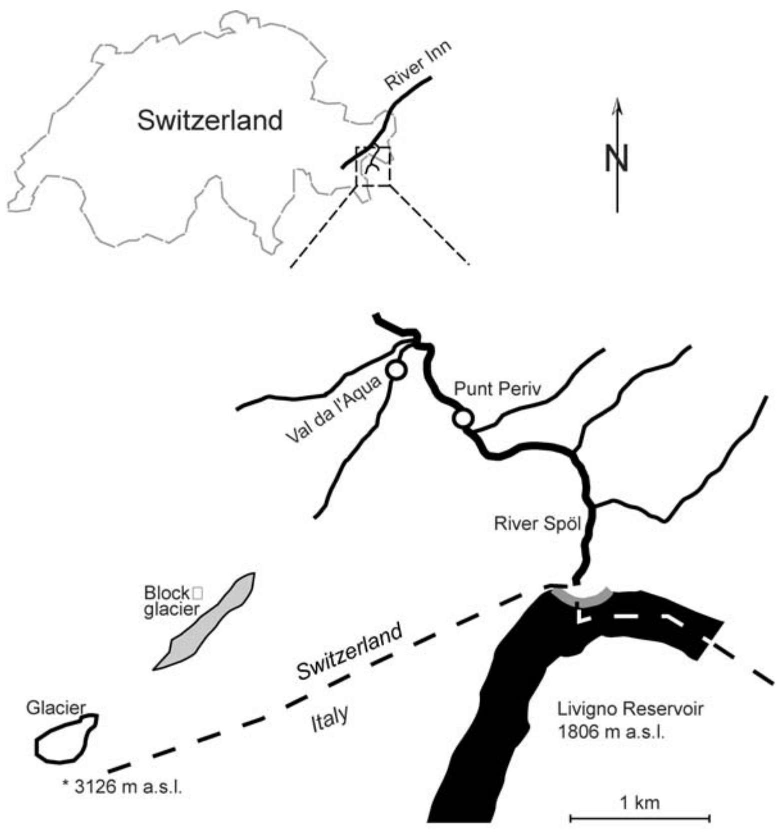

Figure 1. Map of the study sites in the Swiss National Park. The Livigno Reservoir lies on the border of Italy and Switzerland. Reservoir capacity is 164×10^6 m^3.

Table 1. Physical and chemical characteristics of the study sites based on spot measures recorded on each visit during 1999 (n = 7), 2000 (n = 16), 2001 (n = 13), and 2002 (n = 6).

Parameter	Spöl		Val da l'Aqua	
	mean	SD	mean	SD
Catchment area at study site (km^2)	286		4.3	
Catchment area between dam and study site (km^2)	6			
Percent catchment glaciated	1.0		0.2	
Altitude at study site (m a.s.l.)	1660		1750	
Channel slope (range in %)	1–2		5–6	
Channel width (range in meters)	10–18		3–7	
Temperature (°C)	7.6	1.4	4.2	1.2
Conductivity (µS/cm)	248	17	207	44
Turbidity (NTU)	8.3	8.7	9.5	4.5
Nitrate-N (NO_2+NO_3, mg/l)	253	47	247	66
Particulate nitrogen (PN, mg/l)	20.3	9.4	8.3	7.9
Phosphorus (SRP, mg/l)	0.81	1.1	0.57	0.71
Particulate phosphorus (PP, mg/l)	4.7	3.4	2.5	1.6
Silicate Oxide (SiO_2, mg/l) (1999 only)	2.3	0.7	1.4	0.5
Dissolved organic carbon (DOC, mg/l)	0.84	0.36	0.64	0.28

the border between the two countries. The river below the dam flows through a confined canyon and the study reach (Punt Periv) is situated about 2.3 km downstream of the dam (coordinates: 10°11′ N, 46°38′ E). The maximum elevation of the Spöl catchment is 3302 m a.s.l. and is 1660 m a.s.l. at the study site (Table 1). Stream width of the study reach ranged from 10 to 18 m, and stream slope was 1–2%. Stream substrata consisted of alluvial cobbles and boulders with some bedrock outcrops also present. Water temperature averaged 7.6 °C over the four year period with little variability among years.

A reference stream (Val da l'Aqua) was selected that flows into the River Spöl about 0.8 km downstream of the Spöl study reach (Fig. 1). Although the Val da l'Aqua is smaller (width 3 to 7 m) and has a higher gradient (slope 5 to 6%) than the Spöl, it has a natural flow regime and biota adapted to this natural stream environment. Data from this site were used to examine seasonal patterns in macroinvertebrate abundances relative to those in the Spöl. Val da l'Aqua drains a 4.3 km^2 catchment with a small rock glacier (representing 0.2 % of the catchment area) near its headwaters (Table 1). Its catchment has a maximum elevation of 3126 m a.s.l. and the study site was at 1750 m a.s.l. Substrata were mostly alluvial cobbles and boulders. Discharge in Val da l'Aqua averaged 0.38 m^3/s (range: 0.06–0.69 m^3/s; CV = 59%) based on periodic discharge measurements (approximately monthly in spring, summer, and autumn) completed on site (n = 8) from October 1999 through December 2000. Primary water sources are groundwater, snow melt in spring, and melt water from the rock glacier. Water temperature averaged 4.2 °C (range 0–8 °C) over the study period. Water chemistry was similar in both streams during the study period, although particulate nitrogen tended to be greater in the Spöl than in Val da l'Aqua (Table 1).

The experimental floods

Figure 2 shows the discharge regime of the River Spöl in three typical years (1960–1962) before dam construction (full operation in 1974), a typical year after dam construction (1999), and during 2000–2002. The latter included a high flow release in October 2000 caused by heavy precipitation that filled the reservoir beyond its capacity. Following dam construction, the residual flow in the Spöl was 1.5 m^3/s at night and 2.5 m^3/s during the day. After September 1999 discharge in the Spöl was reduced to 0.70 m^3/s until 16 May 2000 when summer base-flow was maintained at 1.6 m^3/s. The reduction in residual flows following September 1999 provided enough water for the floods to be a cost neutral experiment. The experimental flood peaks (m^3/s) were comparable to peaks attained naturally before dam construction, but the average daily flows during each flood were lower than pre-dam values because artificial flow peaks lasted only a few hours. Flow peaks of each experimental flood were 16 m^3/s with a discharge of 10 m^3/s for about 7.5 h on 15 June 2000, peak flow of 43 m^3/s and discharge of at least 25 m^3/s for about 7.5 h on 5 July 2000, and a peak flow of 12 m^3/s with a discharge of 10 m^3/s for about 7 h on 10 August 2000. Similar peak flows were obtained in 2001, but in 2002 the two floods had peaks of >40 m^3/s (July) and ca. 10 m^3/s (August). The peak flow that resulted from excessive precipitation in October 2000 reached 30 m^3/s and extended over 3 days. Average daily discharge was 20 m^3/s during this flood. The rising and receding limbs of each experimental flood were physically constrained by the capacity of the flow control gates.

Field protocols

Field sampling began about one year prior to the experimental flooding in mid-May 1999. Benthic samples (Hess sampler, 0.04 m^2, 100-µm mesh, n = 3) were collected from each 100-m long study reach at intervals between May and November of each year (n = 5 in 1999, n = 15 in 2000 and 2001, n = 6 in 2002). Benthic macroinvertebrates were collected from riffle/run habitats and preserved in the field with 70% ethanol. Study reaches were representative of general stream conditions. In flood years, samples were collected the day before

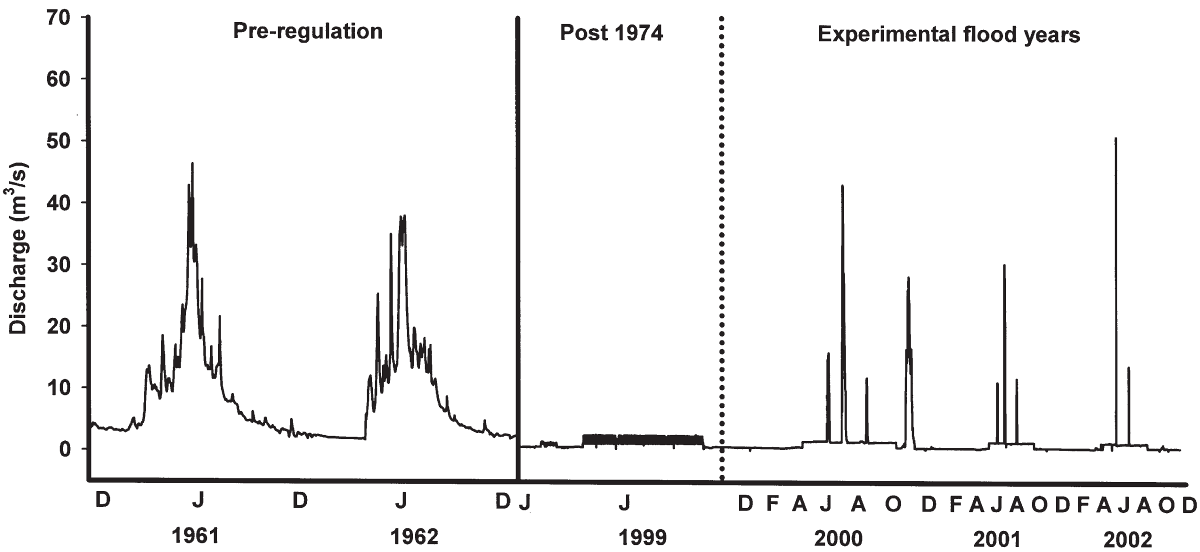

Figure 2. Discharge of the Spöl before construction of the dam (years 1960–1962) and during the 4 years of study, including the year (1999) prior to implementing the experimental flood regime. The flow in 1999 represents the residual flow maintained below the dam with all excess water diverted downstream for power production.

each flood, the day after each flood, and in 2000/2001 at intervals (usually twice) between each flood. Temperature loggers (Vemco Inc., Nova Scotia, Canada) were installed at each site on the first visit and downloaded periodically over the four-year study. Discharge of the River Spöl was recorded by the Swiss Hydrologic and Geologic Survey at Punt dal Gall dam and was measured periodically in Val da l'Aqua using a salt dilution method (Gordon et al., 1992).

On each visit to each site we also collected 1-L water samples for chemical analyses (summarized in Table 1). Turbidity (nephelometric turbidity units, NTU; Cosmos, Züllig AG, Switzerland) and conductivity were measured in the field on each sampling date. Water samples were returned to the laboratory and filtered prior to analyses of ammonium, nitrite-N, nitrate-N, dissolved and particulate N, soluble reactive phosphorus, dissolved and particulate phosphorus, dissolved organic carbon, and particulate organic carbon following methods in Tockner et al. (1997). Silicate (SiO_2) concentrations were determined on some dates ($n = 6$).

Benthic macroinvertebrates were hand-picked from each sample using a dissecting microscope at 10X, identified to lowest practical taxonomic unit (usually genus) and counted. Material remaining in each benthic sample was dried at 60 °C, weighed, combusted at 550 °C, and reweighed to obtain estimates of benthic organic matter (BOM) as AFDM. Data were analyzed using two-way repeated measures ANOVA (site and time as effects) following data transformation (log(X+1)) to improve normality (Zar, 1984). Post-hoc testing was done with Tukey's HSD test. In addition, a principal components analysis (varimax rotated) was completed on the transformed density data to illustrate shifts in assemblage structure among years, and before and after each flood.

Results

Benthic organic matter

The amount of benthic organic matter (BOM) was highly variable in both streams during the study period, and the floods had little noticeable effect on its quantity in the River Spöl (Fig. 3). Average amounts among sampling dates in 1999 ranged from around 8 g/m^2 to over 24 g/m^2 in the Spöl. Values decreased in 2000 and 2001 to less than 12 g/m^2 in the Spöl with similar patterns observed in Val da l'Aqua. BOM increased towards the end of 2001 and into spring 2002 in the Spöl, when the effects of the floods became clear. Before the first flood in 2002, BOM attained values of ca. 24 g/m^2, whereas after this flood BOM quantity decreased to around 2 g/m^2. A similar, although less intense, decrease occurred after the second flood in 2002 (Fig. 3).

Macroinvertebrate response

The density of macroinvertebrates in the Spöl was reduced significantly by each flood ($p < 0.0001$), except for the first flood (Fig. 4). The first flood (2000) had no significant affect on average densities (Tukey's test, $p > 0.05$), although it was apparent from field observations that the impact of this flood was highly patchy with some areas of the stream bottom being heavily scoured and others being minimally affected (C.T. Robinson, pers. observ.). Macroinvertebrate densities were signifi-

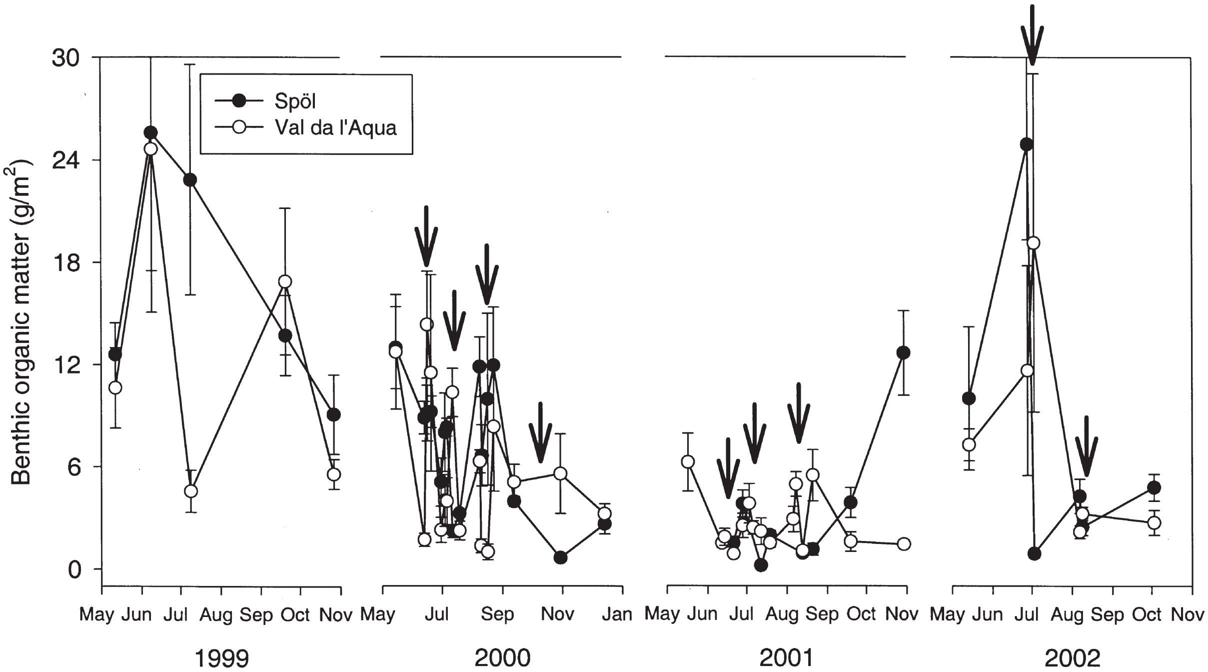

Figure 3. Temporal patterns in the quantity of benthic organic matter (g/m^2) associated with benthic samples collected from Val da l'Aqua and the Spöl on each sampling date during the study period. Symbols represent mean values (n = 3, +1 SE). Arrows indicate the time of each flood.

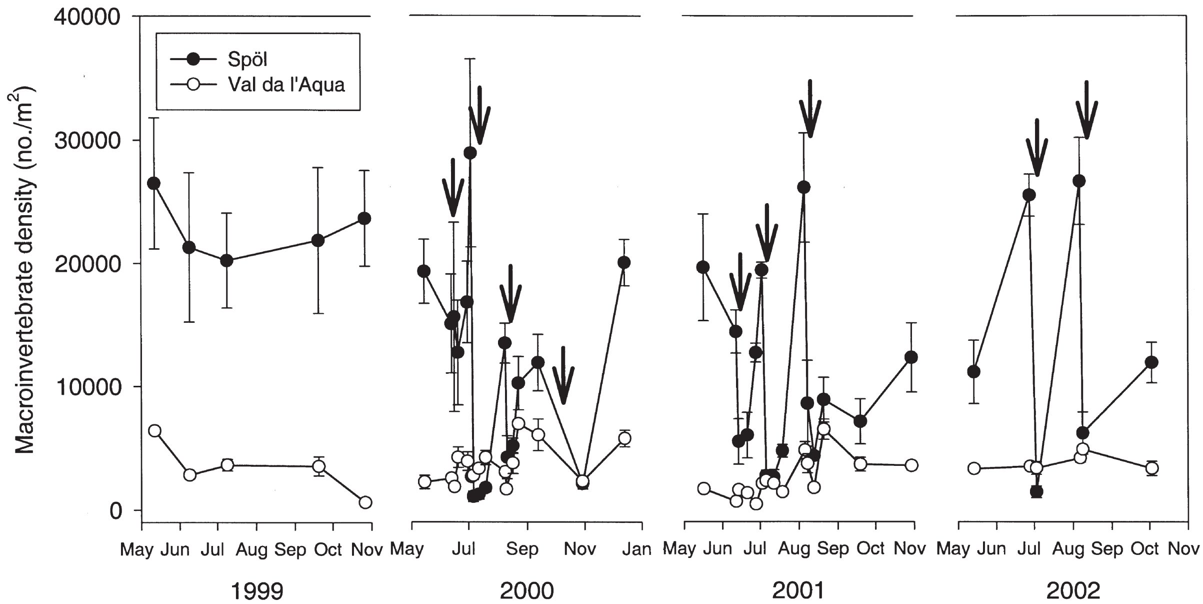

Figure 4. Mean macroinvertebrate density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

cantly lower following each of the following floods ($p < 0.0001$), and there was greater temporal variability in density during the flood years (2000–2002). Maximum densities of macroinvertebrates between floods were similar to pre-flood densities in 1999 (Fig. 4), although the composition of the assemblage changed dramatically over the study period (see below). Densities typically were higher and more variable in the Spöl than in Val da l'Aqua, except immediately following the floods, when densities between the two streams were comparable.

Of the more abundant taxa, gammarids and turbellarians were negatively affected by the floods ($p < 0.0001$) (Figs. 5, 6). Densities of *Gammarus fossarum* typically

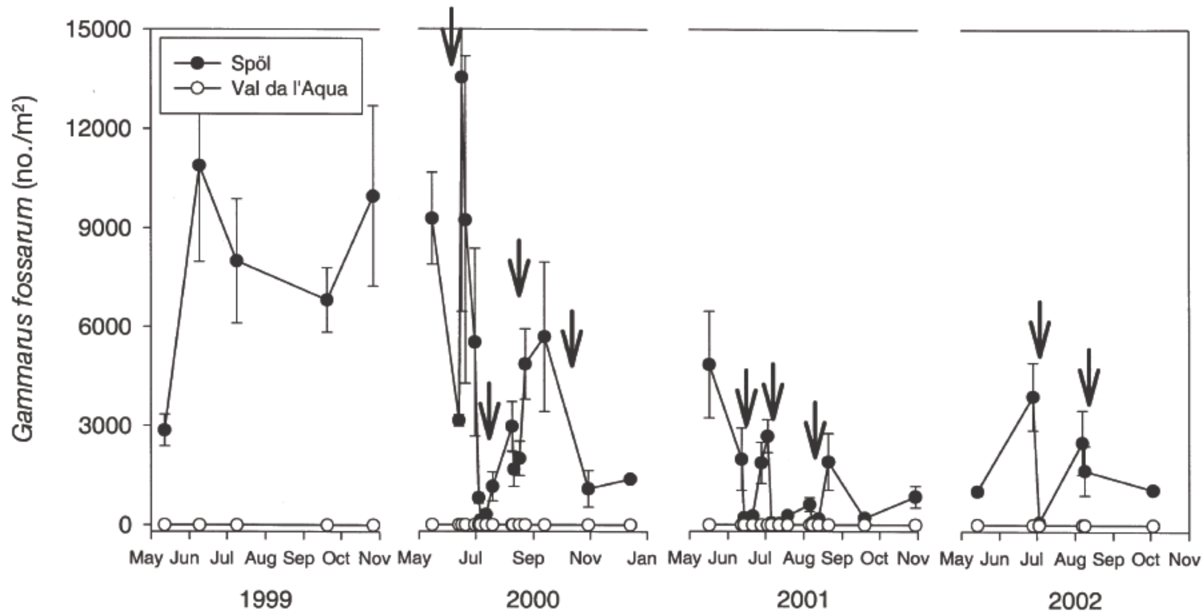

Figure 5. Mean *Gammarus fossarum* density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

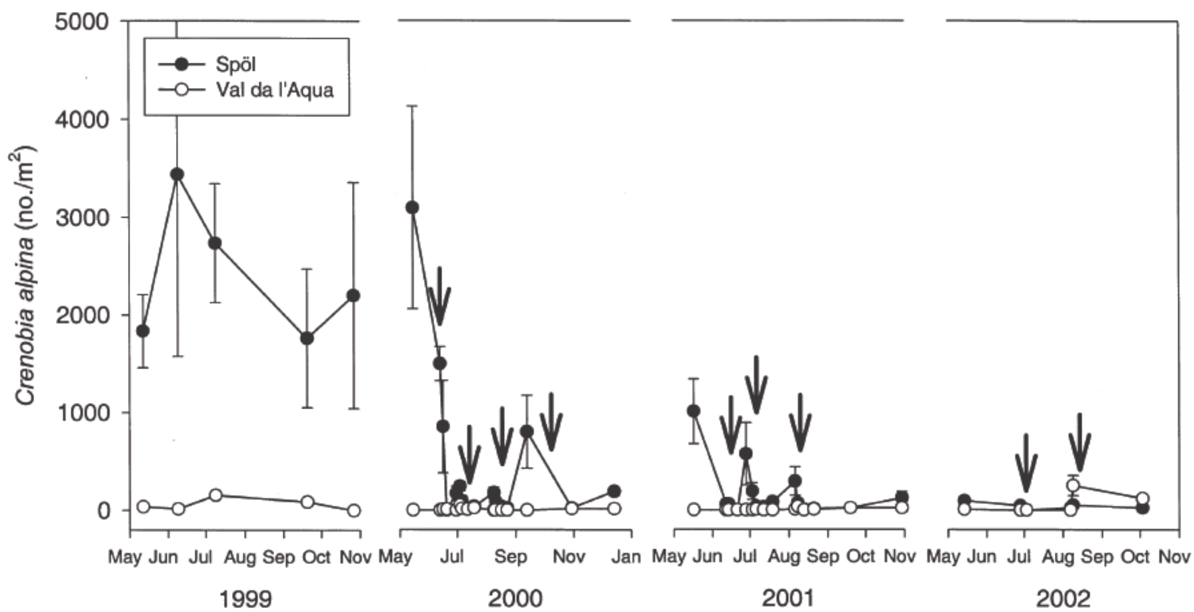

Figure 6. Mean turbellarian (*Crenobia alpina*) density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

were greater than 7000 ind/m² before the floods in 1999 (Fig. 5). Average *G. fossarum* density increased after the first flood, but decreased following the subsequent floods in 2000, with densities typically being below 3000 ind/m². The floods in 2001 and 2002 decreased *G. fossarum* densities, whose maxima were always <3000 ind/m². Gammarids were not present in Val da l'Aqua. The density of the turbellarian *Crenobia alpina* was reduced dramatically following the floods, beginning in 2000 (Fig. 6). Densities in 1999 were usually >2000 ind/m², but they remained below 1000 ind/m² after the first flood in 2000, with little recovery in 2001 and especially in 2002. *Crenobia alpina* densities were similar to those in Val da l'Aqua (<100 ind/m²) by 2002.

Simuliidae (Diptera; *Simulium* and *Prosimulium* spp.) and Baetidae (Ephemeroptera; *Baetis* spp.) increased in

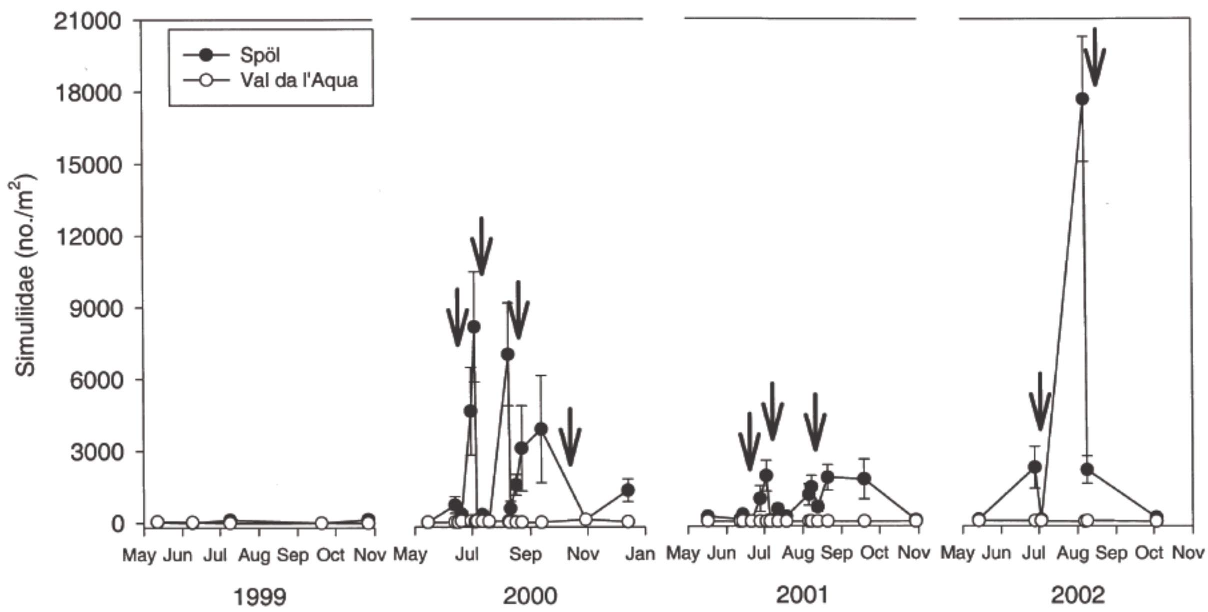

Figure 7. Mean Simuliidae density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

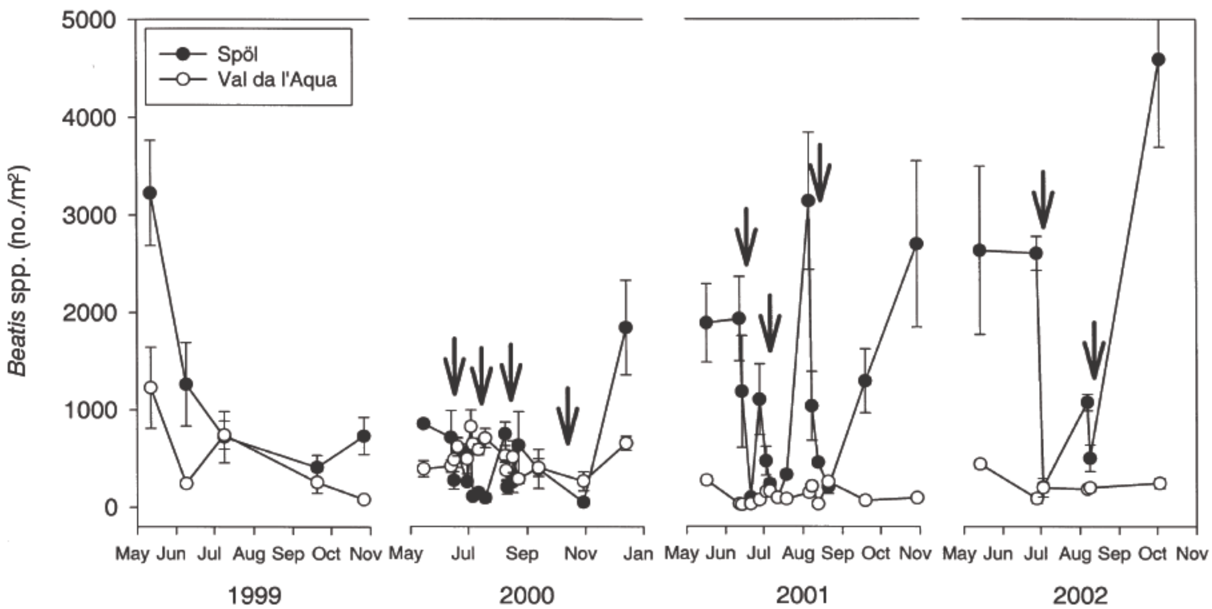

Figure 8. Mean Baetidae (*Baetis* spp.) density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

abundance over the flood years ($p < 0.0001$), suggesting a positive response to changing habitat conditions (Figs. 7, 8). Simuliid densities increased from less than 50 ind/m² in 1999 to over 3000 ind/m² in 2000 through 2002 (Fig. 7). Density reached ca. 18,000 ind/m² in summer 2002, but was reduced to <3000 ind/m² after the August 2002 flood. The floods typically reduced the density of simuliids, but recovery to pre-flood density typically occurred within 10–14 days. Although densities of Baetidae ranged between 1000–3000 ind/m² in 1999, their average densities were usually >2000 ind/m² by 2001 and reached >4000 ind/m² by the end of 2002 (Fig. 8). Like the Simuliidae, the Baetidae decreased in abundance following each flood but recovered within two weeks.

Chironomidae density decreased following each flood ($p < 0.0001$), although recovery was fast and aver-

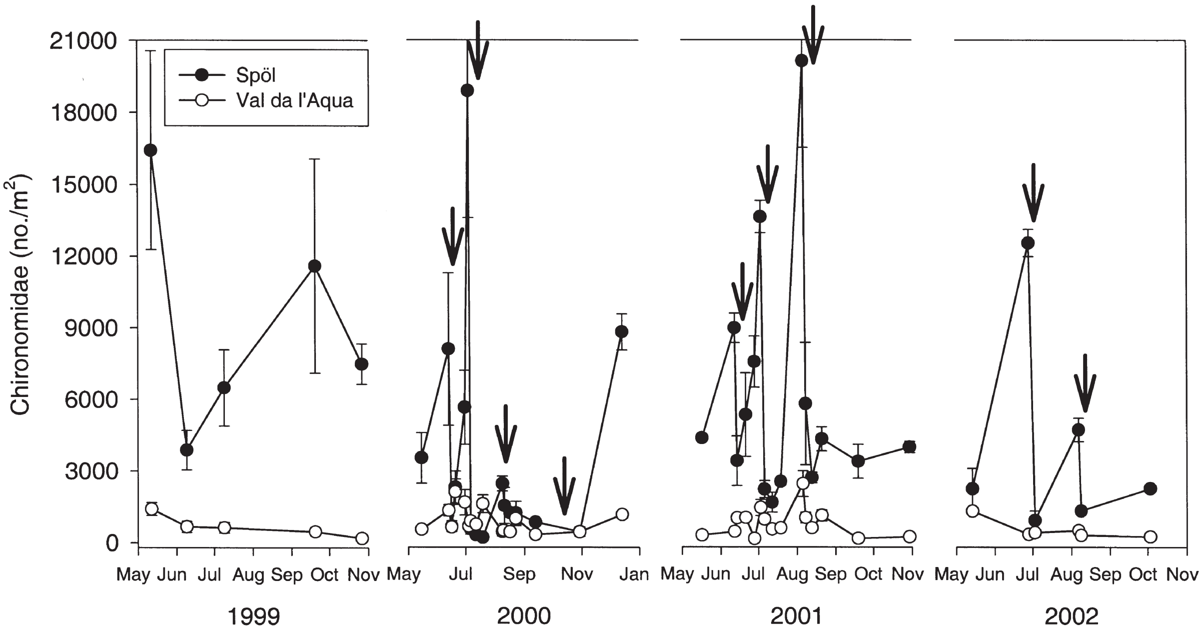

Figure 9. Mean Chironomidae density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

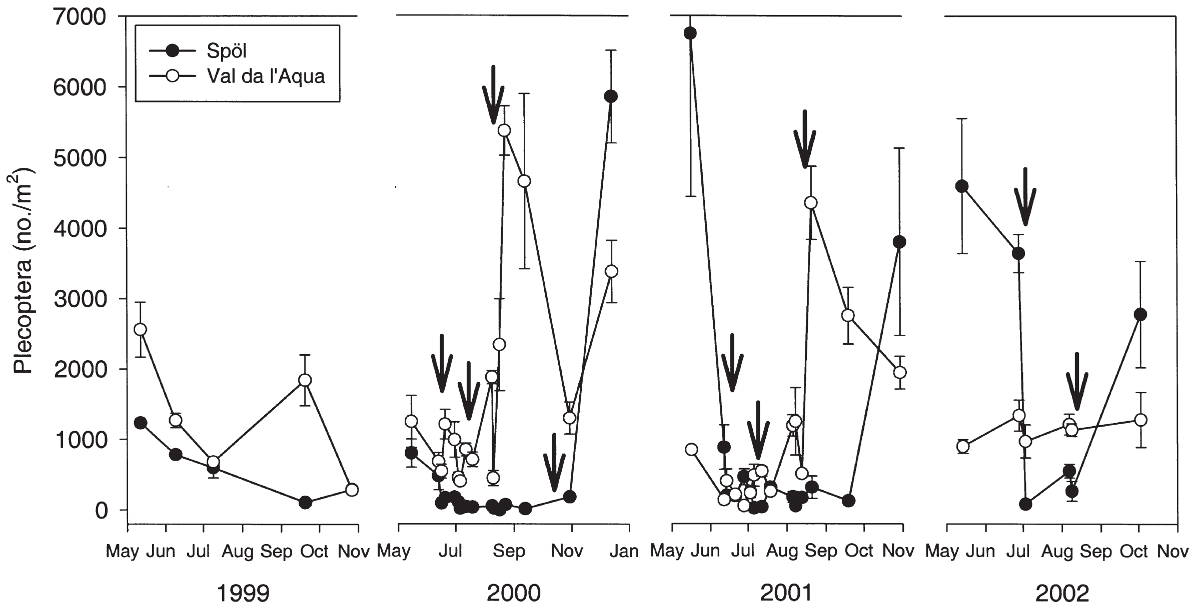

Figure 10. Mean Plecoptera density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

age densities remained similar to those in 1999 (Fig. 9). Thus, although chironomids were abundant in the Spöl prior to the flood years, their overall densities were not reduced by the flood regime. Chironomidae appeared to respond to the floods in a similar manner as the simuliids and baetids; i.e., density reduction by each flood followed by a fast recovery.

Plecoptera (mostly Nemouridae and Chloroperlidae) and Trichoptera (Limnephilidae) exhibited a delayed response to the implemented flood regime (Figs. 10, 11). The Plecoptera displayed low densities in 1999 and for most of 2000 (<1000 ind/m2), increased dramatically in late 2000 (ca. 6000 ind/m^2), decreased in summer 2001, and increased again in autumn of that year. A similar seasonal pattern occurred in 2002 (Fig. 10). Plecoptera den-

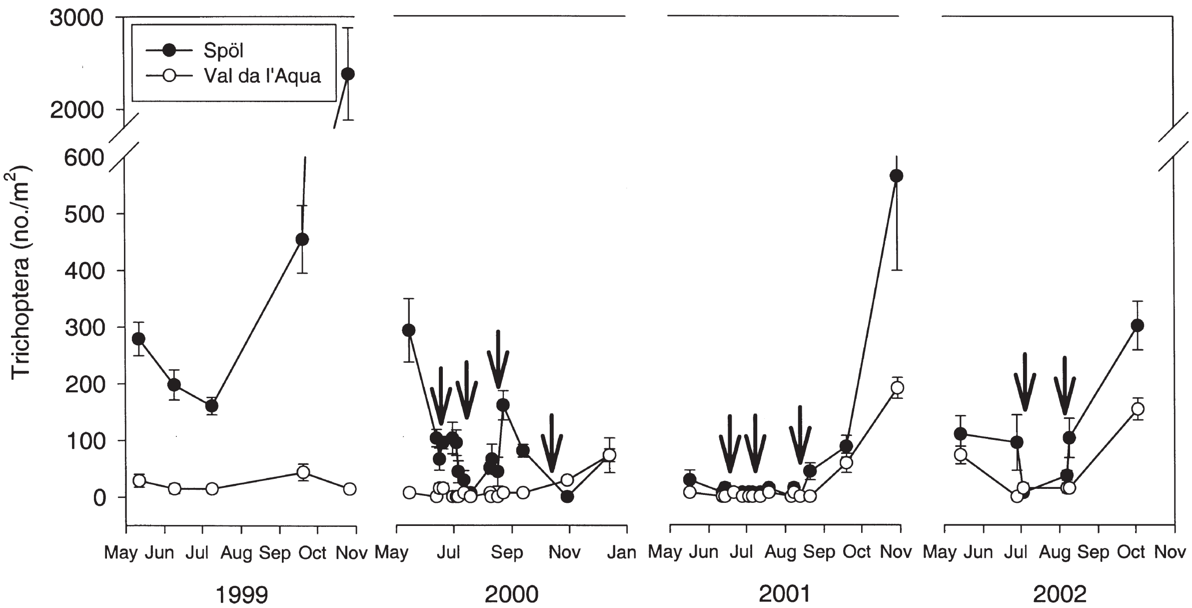

Figure 11. Mean Trichoptera density (n = 3, +1 SE) estimated from benthic samples collected from the Spöl and Val da l'Aqua on each sampling date. Arrows indicate the time of each flood.

sities reached similar high levels in autumn (due to increases in the Nemouridae) in Val da l'Aqua as those in the Spöl. The Trichoptera (mostly the limnephilid *Allogamus auricollis*) showed relatively high densities in the Spöl 1999, reaching ca. 2500 ind/m^2 in autumn 1999 (Fig. 11). The floods in 2000 significantly reduced the abundance of Trichoptera in the Spöl to levels observed in Val da l'Aqua ($p = 0.0003$). However, Trichoptera numbers reached pre-flood levels by the end of 2001 (>500 ind/m^2), and maintained densities of 100–300 ind/m^2 in 2002. Trichoptera densities increased significantly in autumn in both 2001 and 2002 ($p < 0.0001$).

Temporal shifts in macroinvertebrate composition

Results of the principal components analysis illustrate the shifts in assemblage structure resulting from each flood and from the change in flood regime (Fig. 12). In general, the analysis indicated a change in assemblage composition from 1999 to 2000 and from 2000 to 2001/2002. The first two axes explained 62% of the variation in assemblage characteristics over the study period. Axis-1 was associated with the abundance changes in Baetidae, Plecoptera, Diptera, Heptageniidae, and Chironomidae, whereas axis-2 was associated with density changes in Gammaridae, Turbellaria, and Trichoptera. The plot shows that the first flood (2000) reduced the contribution of taxa explained by axis-1, whereas the next two floods in 2000 were important in decreasing the abundances of taxa along axis-2. Taxa along axis-2 continued to decrease in 2001/2002, whereas taxa along axis-1 increased in prominence (a shift to the right from 2000 to

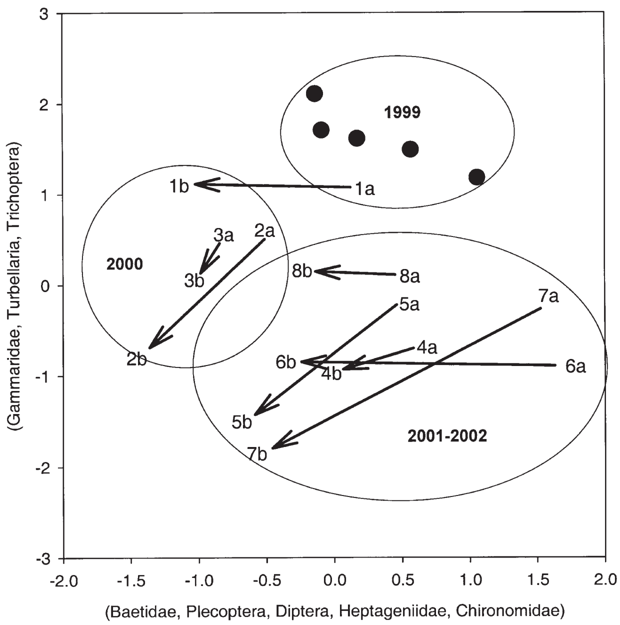

Figure 12. Scatterplot of the principal components analysis results based on the densities of macroinvertebrate taxa in the Spöl. Data plotted represent assemblages during 1999 and before and after each flood in 2000 through 2002. Symbol numbers arranged by flood sequence (e. g., 1 = first flood in 2000) where 'a' and 'b' are before and after each flood, respectively. Taxa listed along each axis had a factor loading of 0.7 or greater. Axis-1 explained 38% of the variation among samples and axis-2 explained 23% of the variation. Circles are drawn simply for illustration purposes.

2001/2002) (Fig. 12). The floods in 2001/2002 appeared to mostly reduce the abundances of taxa along axis–1 (a shift to the left after each flood), although recovery of axis–1 taxa was substantial as suggested by the relative length of the arrows in the plot.

Discussion

General response patterns

The macroinvertebrate assemblage as a whole, responded to each flood in a predictable fashion with macroinvertebrate densities being reduced substantially following each flood. An exception to this general response was observed following the first low magnitude flood (June 2000, discharge ca. 10 m^3/s), when average densities remained unchanged despite the distribution of macroinvertebrates being highly patchy. Thus, Robinson et al. (2003) found that the sample coefficient of variation before this flood was 64 %, whereas it was 148 % the day after the flood. They observed some areas of the stream bed to be essentially unaffected by the high flows, whereas others were heavily scoured. This particular response has been observed by others studying the effects of floods on zoobenthos (Palmer et al., 1995; Matthaei et al., 1999a, b), and it is probable that the less disturbed areas act as refugia for macroinvertebrates during a flood (Francoeur et al., 1998). The second larger flood, in contrast, mobilized most of the stream bed and we observed few areas of the study reach that were left undisturbed. We suspect that the first flood removed many of the fine sediments in the Spöl, causing the stream bed to become more susceptible to physical disturbance from the next flood (concomitant with the greater competence of the larger second flood). In many respects, the second large flood in 2000 showed similar effects to those found following catastrophic spates in arid and pre-alpine streams (Grimm and Fisher, 1989; Uehlinger et al., 1996).

Following the initial flood year, the response by macroinvertebrates to floods was quite similar in years 2 and 3. The data indicated that a shift in assemblage composition had occurred by 2001, and that a similar assemblage was present in 2002. Taxa associated with more stable habitat conditions were reduced in abundance (e.g., gammarids and turbellarians), whereas taxa considered disturbance-resistant (e.g., chironomids, simuliids) were becoming more abundant over time. This change in assemblage structure was reflected in the faster recovery responses observed in 2001 and 2002. For example, overall abundances decreased during 2000 (the first year of flooding) in concert with density decreases in gammarids and turbellarians, although simuliid and chironomid populations recovered quickly, even in this first year. The subsequent floods successfully maintained populations of gammarids and turbellarians at low levels relative to pre-flood densities. In contrast, besides chironomids and simuliids being common constituents of the assemblage, baetids and various Plecoptera increased in abundance and appeared to respond favorably to the flood regime. Some other taxa, including heptageniid mayflies (*Rhithrogena* spp.) and Trichoptera, also were beginning to increase in numbers in the presence of floods, although it remains to be seen whether the assemblage present in 2002 is maintained in the face of further flooding. The data clearly indicate that a flood regime needs to be maintained to sustain the present trajectory in assemblage composition, otherwise the system may quickly return to pre-flood characteristics.

The results of our study are probably indicative of conditions in most confined rivers below dams. The lateral displacement of water is reduced in confined channels relative to unconfined channels (Badri et al., 1987), causing a high degree of scouring and the dislodgement and drifting of organisms (Irvine and Henriques, 1984; Imbert and Perry, 2000). Lytle (2000) suggested many of these drifting organisms are delivered downstream, although many others may accumulate in slow flow areas, or shorelines (Winterbottom et al., 1997). In the Spöl, we observed many macroinvertebrates in the drift during the floods and many organisms (especially *G. fossarum*) stranded following flow reduction after each flood (Aebischer, 2001; Robinson et al., unpubl. data). Perry and Perry (1986) also noted that shorelines may act as traps, stranding high numbers of organisms once flood flows recede. Others have observed that some invertebrate taxa actively enter the drift in response to changes in flow (Williams and Winget, 1979; Hart and Finelli, 1999; Holomuzki and Biggs, 1999; Gayraud et al., 2000). Of interest is that drifting and stranding were evident in all three years of flooding, despite assemblage composition shifting to more disturbance resistant taxa. Whether a similar response would be found in unconfined rivers subject to flooding has yet to be tested.

Taxon-specific responses

Taxon-specific responses became apparent over the four-year study period. Gammarids and turbellarians, which are indicative of more stable habitat conditions, were negatively affected by the flood program. However, both taxa still maintained populations, albeit in low numbers, in the Spöl after three years of flooding, indicating that habitats suitable for sustaining population recruitment are still present. Another possibility is that individuals from adjacent tributaries quickly recolonize the Spöl following each flood. The turbellarians exhibited a more rapid response and slower recovery to the floods than the gammarids, probably reflecting the fact that turbellarians are crawlers, whereas gammarids are strong swimmers (Hynes, 1970). This difference in mobility probably makes recolonization of turbellarians from tributaries much slower than that of gammarids. Regardless, the flood regime appears to simply reduce population sizes of these groups without eliminating them from the system.

Other long-lived (univoltine or semivoltine) taxa, including some trichoptera (e.g., *Allogamus auricollis*) and heptageniids, were reduced or even eliminated during the first year of flooding. Many trichopteran larvae clearly were damaged by the scouring action of the floods, which destroyed cases (numerous dead and living individuals without cases were observed following the first floods) and, thereby, increasing their susceptibility to damage and death. Dobson et al. (2000) found that some trichopteran larvae actually abandon their cases when subject to disturbance such as burial by sediments, a highly energetically costly behavior. It is unclear why the heptageniids were reduced as they are good swimmers, although a possible explanation is that their negative phototactic behavior of residing on the sides and bottoms of stones increased their mortality by scouring. Nevertheless, both groups had recolonized the Spöl by year 3 and appear to be relatively common. Further, members of these groups are commonly found in streams with a natural flood regime (Robinson and Minshall, 1998; Burgherr et al., 2002), thus we would expect them to be present following an initial adjustment period to the new flow regime in the Spöl. Both are present in Val da l'Aqua, a system subject to periodic flooding, thus supporting this premise.

Some taxa, although clearly reduced in abundance following each flood, were little affected over the 3 year period of flooding. Baetids, in particular, demonstrated high resilience to each flood, becoming a numerically dominant group in years 3 and 4. Simuliids and chironomids, as mentioned above, also showed high resistance to each flood, at times increasing in abundance by >18,000 ind/m^2 within days following a flood. All three groups exhibit traits allowing the quick recolonization of denuded habitats (Robinson and Minshall, 1986; Matthaei et al., 1996a). The Plecoptera were initially low in abundance in the Spöl before the floods, but subsequently attained rather high densities. This group also demonstrated a degree of seasonality, with relatively low numbers in summer when numerous adults were observed in flight, and high densities in spring and autumn. Consequently, populations are likely to be little affected by the floods in summer, and possibly capitalize on increased resources due to the reduction of other taxa from the floods. Their life histories are similar to those of taxa in arid streams subject to frequent flooding with many species being present in the terrestrial adult phase during the flood period (Fisher et al., 1982; Boulton et al., 1992).

In summary, the experimental flood regime appeared to have a beneficial effect on the structural properties of the macroinvertebrate assemblage. Taxa dominating the assemblage have been reduced in numbers and other taxa have increased their abundances. Southwood (1988) argued the importance of the habitat templet in dictating assemblage structure, and lotic ecologists have shown that disturbance (Resh et al., 1988), and the flow regime in particular (Poff et al., 1997), are important components of the habitat templet in stream ecosystems. Our study has shown that disturbance in the form of floods can be used as an effective management tool that incorporates a strong theoretical and empirical foundation in stream ecology. Whether assemblage structure is maintained by the flood program has yet to be determined, but we suspect that assemblage trajectories will change over time as new species colonize the Spöl from other sources. Lastly, this study was conducted on a confined river below a large dam, thus other studies are needed to adequately test the findings on rivers in different geomorphological settings.

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