

Flooding plays an important role in regulating the distribution, abundance, and coexistence of benthic macroinvertebrates in many lotic systems (Resh et al. 1988, Poff and Ward 1998, Lake 2000). Significant decreases in macroinvertebrate densities have been recorded after bed-scouring floods (Giller et al. 1991, Lytle 2000, Maier 2001, Robinson et al. 2003a, b), but macroinvertebrate communities are generally highly resilient (Townsend et al. 1987, Boulton et al. 1992) and usually recover to preflood densities within a few weeks or months (Badri et al. 1987, Mackay 1992, Matthaei et al. 1997, Robinson et al. 2003a, b). These recovery periods are shorter than the generation times of most species, and this pattern suggests that organisms use morphological, behavioral, and physiological traits (Statzner and Holm 1982, 1989, Waringer 1989), as well as spatial flow refugia (Palmer et al.

1995, Rempel et al. 1999, Lancaster 2000), to survive floods. It is not known whether similar responses to floods occur in flow-regulated rivers, where a suite of organisms different from the suite that was present before regulation predominates after regulation, nor is it known whether response patterns change with sequential floods. These questions are important because managed-flow regimes using experimental floods are being implemented in some regulated rivers to restore ecological integrity (Poff et al. 1997) and biotic assemblage structure (Robinson and Uehlinger 2003).

Floods usually cause an increase in suspended organic matter, inorganic sediments, and macroinvertebrate drift (Imbert and Perry 2000). Concentrations of suspended organic matter and inorganic sediments tend to follow a typical hysteresis pattern during a flood; concentrations increase on the rising limb and decrease on the declining limb of the hydrograph (e.g., Lenzi and Marchi 2000). However, the spatial and temporal patterns associated with responses of liv-

ing macroinvertebrates to floods are not well known, particularly with respect to the transfer of organic matter (seston) and macroinvertebrates (drift) to lateral habitats (areas of the floodplain adjacent to the stream that become inundated during floods) during flooding (Rempel et al. 1999). Catastrophic drift would be an expected initial response if the flood caused bed movement, and later responses might include behavioral drift if organisms redistribute themselves in response to changing habitat and flow conditions (Perry and Perry 1986).

The existence of flow refugia within a stream channel implies that the increase in hydraulic stress caused by flooding is heterogeneous or patchy in space. Flow refugia that occur at fine spatial scales include patches of woody debris within channels (Palmer et al. 1996) and different types of substrata (Downes et al. 1998), whereas refugia at larger scales include flooded riparian areas (Prévoit and Prévoit 1986, Badri et al. 1987, Rempel et al. 1999) or flow-protected areas within the stream (Matthaei and Townsend 2000). For instance, in cobble- and gravel-dominated riffles of upland streams, individual stones at the same site had different probabilities of being disturbed during floods (Downes et al. 1998, Matthaei et al. 2000). At a larger scale, pools, riffles, and runs are differentially affected by changes in flow, and each habitat has a relatively distinct cast of macroinvertebrates with different susceptibilities to flow disturbance (e.g., Lytle 2000). Recovery of macroinvertebrates following floods probably depends on how different coarse-scale habitats function as refugia for macroinvertebrates during floods. For example, macroinvertebrates can accumulate in refugia provided by flooded side channels by passive or behavioral dispersal in the drift during floods (Matthaei and Townsend 2000), but they may become stranded and die from desiccation when waters recede (Perry and Perry 1986).

The objectives of our study were to: 1) assess response patterns of organic and inorganic matter and macroinvertebrates during a series of separate, experimental floods that occurred over a 2-y period, 2) measure lateral dispersion of organic matter and macroinvertebrates (drift and benthic abundances) into the flooded riparian area of the stream during floods of different magnitude, 3) test whether macroinvertebrates

responded in a typical hysteresis pattern during floods and monitor changes in these patterns with sequential floods, and 4) investigate whether different coarse-scale habitat types (pools, runs, bedrock, or riffles) provided refugia for macroinvertebrates during floods and assess how the effectiveness of these habitats as refugia varied with flood magnitude and sequence.

Study Area

The study was conducted in the Swiss National Park on the Spöl River downstream of the Livigno Reservoir, which lies on the border of Switzerland and Italy (Fig. 1). The river flows through a confined canyon (Punt dal Gall) just downstream of the reservoir dam. Before the dam was built, baseflow discharge was 6 to 12 m³/s, and peak flows reached 120 m³/s (Scheurer and Molinari 2003). After completion of the dam in 1970, residual flows ranged from 0.55 m³/s in winter to 2.5 m³/s in summer. Since 2000, residual flows have ranged from 0.55 m³/s in winter to 1.45 m³/s in summer. Two flushing flows (each ~35 m³/s) were implemented in 1979 and 1990, and a smaller release of 10 m³/s occurred in 1985. In 1999, the National Park and the local power company (Engadiner Kraftwerke) agreed to implement an experimental flood program to enhance ecological conditions in the river (Scheurer and Molinari 2003). The program consisted of releasing 5 separate floods in June, July, and August 2001 and July and August 2002. In 2001, peak discharge was ~12 to 16 m³/s during the June and August floods and 31 to 44 m³/s during the July flood. In 2002, peak discharge was 52 m³/s during the July flood and 14 m³/s during the August flood. Each flood lasted ~9 h and consisted of an initial 1 to 2 h increase to maximal flow, a 2 to 4 h period at maximum flow, and a continuous 3 to 4 h decrease in flow (see Scheurer and Molinari 2003 for a technical description of each flood). Our study was conducted during these 5 floods.

The study reach (Punt Periv) is ~2.3 km downstream of the dam (lat 10°11'22"N, long 46°36'38"E) at 1660 m above sea level (Fig. 1). The reach is accessible only by trail because of steep canyon walls downstream of the reservoir. Water temperature (Minilog temperature logger, Vemco, Inc., Shad Bay, Nova Scotia) in the study

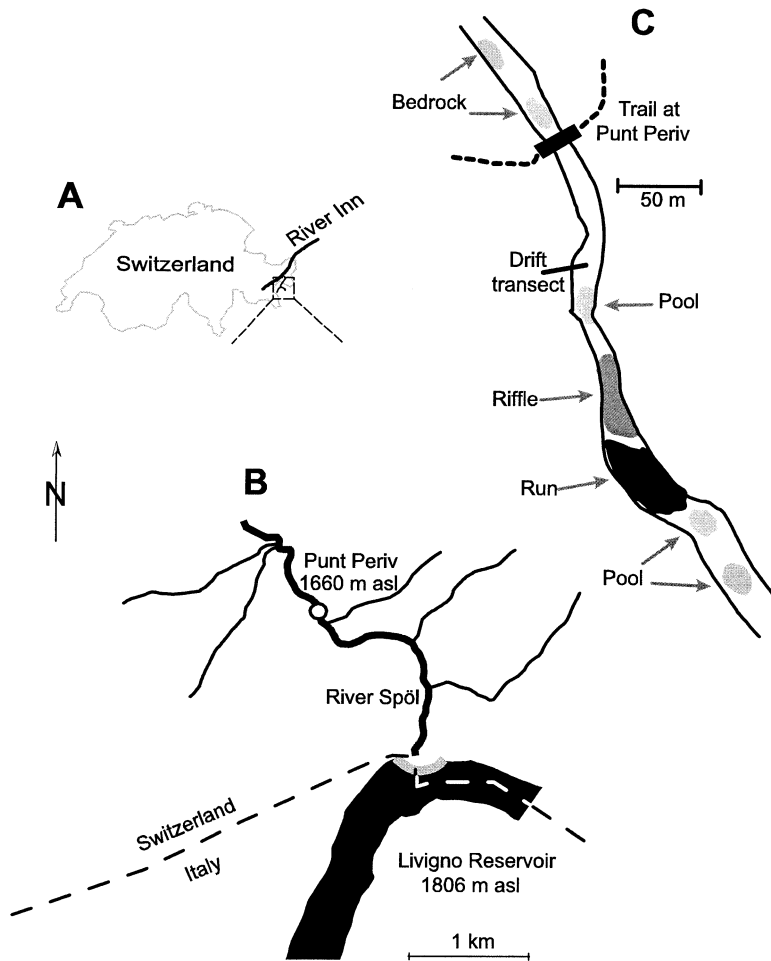


FIG. 1. Study area in the Swiss National Park. A.—Location of the study area in Switzerland. B.—The reservoir dam (gray arc) straddles the Swiss-Italian border, and the study section was located ~2.3 km downstream of the dam at Punt Periv. C.—Schematic diagram of the study reach at Punt Periv showing the location of the transect used for seston and drift sampling during the floods relative to the respective habitat types assessed before and after floods. asl = above sea level.

reach has averaged 7.6°C since 1999 and varies little among years because of hypolimnetic water release from the reservoir. The stream slope along the 300-m study reach is 1 to 2%, and channel width ranges from 10 to 18 m. The stream water is relatively clear with turbidity averaging 8.3 NTU. Dominant substrata consist of gravel/cobble (10–15 cm, b-axis) and boulders (30–60 cm, b-axis) with sporadic patches of bedrock. Bedrock areas are relatively common (~10–15% of the channel bed) because of the canyon-confined condition of the river. The riparian vegetation consists of subalpine conifer

forest dominated by pine (*Pinus mugo*) and fir (*Picea excelsa*).

Methods

Seston and macroinvertebrate drift in riparian areas during floods

Sample collection.—Seston and macroinvertebrate drift samples were collected using drift nets (15-cm width × 30-cm depth, 400- μ m mesh, 1-m long) staked into the stream bottom in a ~25-m-wide section of the river that be-

came fully inundated during each flood (Fig. 1). Drift nets were installed at each station near the surface of the water column to include surface drift during sampling. Velocity was recorded in the center of each net at the time of sampling using a MiniAir2 velocity meter (Schiltknecht AG, Gossau, Switzerland), and was used to calculate the volume (m^3) of water filtered through each net.

The wetted channel width at baseflow was ~ 12 m, and floods raised the water level 0.4 to 0.7 m in this section of the river. Vegetation was sparse along the river margin in this area, although small patches of grass were present; substrata consisted mostly of sand and coarse gravel (5–15 cm in width). Five sampling stations were established along a lateral transect oriented perpendicular to the direction of river flow. The 1st station (S-1) was situated in the thalweg of the main channel at baseflow and was used to collect samples at baseflow and during the first flood in 2001. For safety reasons, drift was not collected at this station during the peak flow of the other floods. The 2nd station (S-2) was situated at the baseflow shoreline, and the 3rd (S-3) and 4th (S-4) stations were situated 3.5 and 7.0 m inland from the baseflow shoreline, respectively. A 5th sampling station (S-5), 10 m from the baseflow shoreline, also was used during the first flood in 2001.

Samples were collected 15 to 30 min before, periodically during, and 15 to 30 min after the 3 floods in 2001 and the July flood in 2002. Individual drift samples were collected every ~ 30 to 40 min on the rising limb of each flood and every ~ 90 min during the falling limb at each station. During each flood, drift samples were collected as close in time as possible from each station on each sampling interval. Individual drift samples were collected over periods of 1 to 2 min depending on how quickly the nets became clogged with transported sediments. This sampling scheme yielded 32 samples (on average) during each flood. Three additional drift samples were collected at baseflow in the thalweg (S-1) on the evening (ca 1800 h) and morning (ca 0730 h) before each flood.

Drift samples were stored in Whirl-Pac[®] bags and frozen (-25°C) until processed. In the laboratory, all invertebrates were hand-picked from each sample using a dissecting microscope at $10\times$ magnification, identified to family or order, and counted. The remaining material (i.e., ses-

ton) from each sample was dried at 60°C , weighed, combusted at 550°C , and reweighed for ash-free dry mass (AFDM) determinations.

Data analysis.—Lateral patterns of abundance and distribution of seston and macroinvertebrate drift during each flood were assessed graphically. Statistical comparisons were not made because only one sample was collected at each station each sampling time. To evaluate whether temporal patterns of abundance in the drift changed with sequential floods (i.e., between early and late floods), seston and drift samples taken at the same time were combined, regardless of location on the transect. Differences in temporal patterns of macroinvertebrate density and seston AFDM in the drift among floods were tested using 2-way factorial analysis of variance (ANOVA) (time and flood as factors) followed by Tukey's test when significant differences were detected (Zar 1984). Macroinvertebrate densities and AFDM were $\log(x + 1)$ transformed to meet the assumptions of the ANOVA. The total number of macroinvertebrates entrained during each flood was estimated by summing the number of animals in the drift (density \times discharge) every 30 min over 9 h for each flood. A 9-h time period was used to facilitate comparison among floods.

Benthic macroinvertebrates deposited and stranded in riparian areas during floods

Sample collection.—Deposited benthic macroinvertebrates were collected from flooded lateral habitats with a Hess sampler (0.016 m^2 , $400\text{-}\mu\text{m}$ mesh) at 90-min intervals during the 3 floods in 2001. Samples were collected from locations at the same lateral distances as drift stations S-2, S-3, and S-4. The first set of samples was collected ~ 20 m downstream of the drift transect and subsequent samples were collected 2 m upstream from each preceding sample location. In this way, subsequent samples were not influenced by any of the preceding sample collections. This sampling scheme yielded 18 to 20 lateral benthic samples during each flood.

Immediately following each flood in 2001, stranded macroinvertebrates were collected from isolated bodies of standing water in the riparian zone near the drift transect. No effort was made to avoid locations that had been sampled for drift or deposited macroinvertebrates. Single Hess samples were collected from 5 different

water bodies. The Hess sampler was used to delineate the sample area and the invertebrates enclosed within the sampler were pushed into the collection net by hand.

All benthic samples were stored in Whirl-Pac® bags and frozen (-25°C) until processed. In the laboratory, all invertebrates were hand-picked from each sample using a dissecting microscope at $10\times$ magnification, identified to family or order, and counted.

Data analysis.—Lateral patterns of abundance and distribution of benthic macroinvertebrates deposited in riparian areas during each flood were assessed graphically. Statistical comparisons were not made because only one sample was collected at each station on each sampling time during the flood. To evaluate whether temporal patterns of abundance changed with sequential floods (i.e., between early and late floods), benthic samples taken at the same time were combined, regardless of location. Differences in temporal patterns of benthic densities among floods were tested using 2-way factorial ANOVA (time and flood as factors) followed by Tukey's test when significant differences were detected (Zar 1984). Benthic macroinvertebrate densities were $\log(x + 1)$ transformed to meet the assumptions of the ANOVA.

Differences in densities of *stranded* macroinvertebrates were not analyzed statistically, but the data are presented for comparison with the densities of deposited macroinvertebrates and as an indicator of the magnitude of the number of invertebrates transported into the adjacent riparian area during floods.

Habitat-specific response of macroinvertebrates to flooding

Sample collection.—Benthic macroinvertebrates were collected from 3 pools, 1 run, 1 riffle, and 2 bedrock reaches (Fig. 1) to test for habitat-specific differences in retention of macroinvertebrates during all 5 floods (i.e., to determine whether habitats were flow refugia). Mean water velocity, substratum size, slope, water depth, and habitat width were used to define the different habitats. Ten benthic samples (Hess sampler, 0.016 m^2 , $400\text{-}\mu\text{m}$ mesh) were collected randomly from each habitat type the day before and the morning after each flood. Benthic samples were stored in individual Whirl-Pac® bags

and frozen (-25°C) for later processing in the laboratory (see above).

Data analysis.—Total macroinvertebrate density and the proportional representation of Chironomidae, Gammaridae, Simuliidae, Ephemeroptera, and Plecoptera in each habitat before and after each flood were assessed using 3-way factorial ANOVA (before/after, habitat, flood) followed by Tukey's test when differences were found (Zar 1984). Initial taxonomic differences among habitat types were tested with ANOVA (Zar 1984). Benthic macroinvertebrate densities were $\log(x + 1)$ transformed to meet the assumptions of the ANOVA.

Results

Seston and macroinvertebrate drift in riparian areas during floods

Lateral patterns.—Samples collected near the shoreline of the baseflow channel (S-2) had higher seston AFDM than samples collected farther from the thalweg (S-3, S-4, S-5) only during the June 2001 flood (Fig. 2). There were no clear differences with lateral position along the transect in seston or macroinvertebrate drift during the other floods. Mean densities of macroinvertebrates in the drift ranged from 250 to $>1300\text{ ind./m}^3$ and varied markedly among sampling stations during and among floods (Fig. 3).

Temporal patterns.—The concentration of seston AFDM in transport increased significantly during the initial stage of each flood (2-way ANOVA, $p < 0.0001$) and decreased to base levels after ~ 2 to 3 h (Fig. 3). An exception occurred during the large flood in July 2001 in which a 2nd peak in seston AFDM was evident in the final hours of the flood. The July 2001 flood peaked at $50\text{ m}^3/\text{s}$ and had significantly higher seston AFDM than the other floods (Tukey's test, $p < 0.05$).

The density of macroinvertebrates in the drift increased significantly during the initial stages (1–3 h) of each flood (2-way ANOVA, $p < 0.0001$) (Fig. 3). Peak drift usually lasted <3 h during each flood and returned to baseflow levels after ~ 4 h into each flood regardless of flood magnitude. No secondary peak in drift was observed during the July 2001 flood.

Average peak densities were ~ 1200 to $1300/\text{m}^3$ during the first 2 floods and 250 to $600/\text{m}^3$ in the 2 subsequent floods.

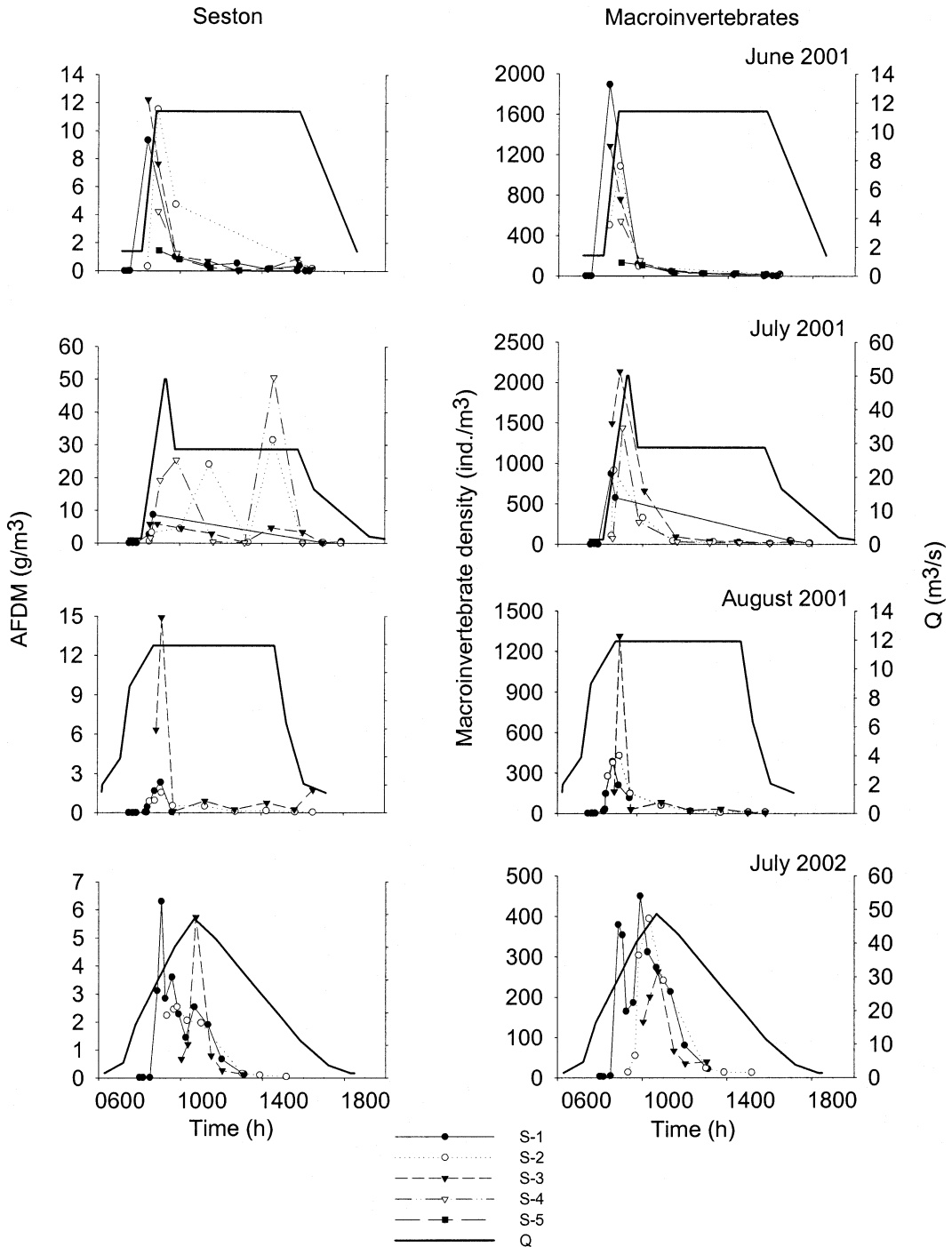


FIG. 2. Seston ash-free dry mass (AFDM) (left column) and macroinvertebrate density (right column) in the drift at each lateral sampling location (S-1 to S-5) with respect to discharge (Q) and time during 4 experimental floods. Discharge is shown on the right y-axis of each panel. See text for description of each lateral sampling location listed in the legend. Note that the y-axis scales differ among floods.

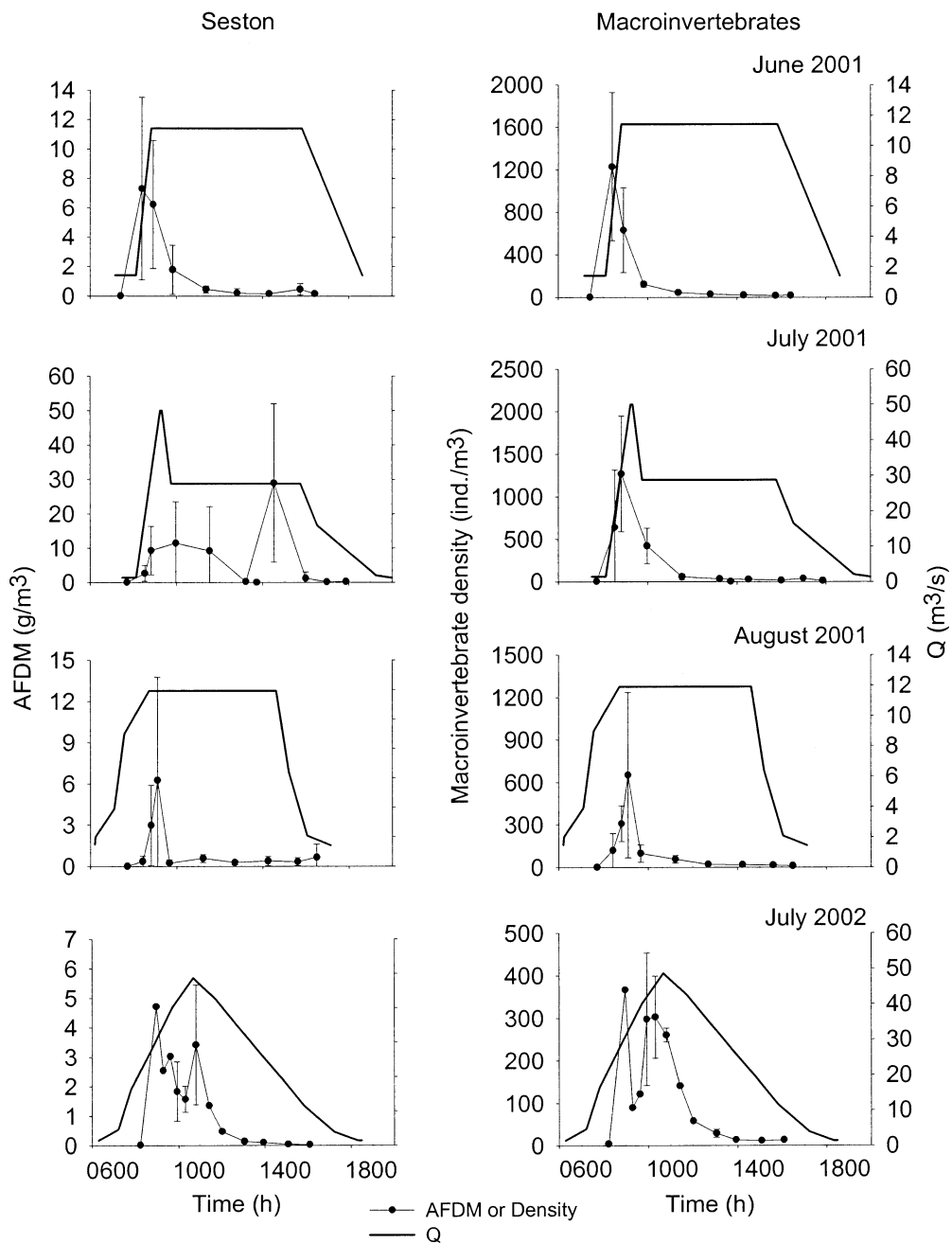


FIG. 3. Mean (+1 SD) seston ash-free dry mass (AFDM) (left column) and macroinvertebrate density in the drift (right column) during 4 experimental floods. Sample means were calculated across all lateral sampling stations for each time ($n = 3-4$). Discharge (Q) is shown on the right y-axis of each panel. Note that the y-axis scales differ among floods.

TABLE 1. Number ($\times 10^3$) and proportional representation (% of all individuals) of the most common taxonomic groups of macroinvertebrates in the drift during 4 experimental floods in the Spöl River in 2001 and 2002. Each flood lasted 9 h.

Taxon	June 2001		July 2001		August 2001		July 2002	
	Number	% of total	Number	% of total	Number	% of total	Number	% of total
Chironomidae	27,663	69	200,850	66	27,491	84	61,493	53
Gammaridae	7658	19	70,026	23	2318	7	30,719	26
Simuliidae	625	2	15,313	5	1948	6	2901	2
Ephemeroptera	1163	3	6568	2	276	1	6992	6
Plecoptera	2072	5	5956	2	261	1	12,214	10
Other	658	2	5338	2	392	1	2660	2
Total	39,839	100	304,051	100	32,686	100	116,978	100

The total number of macroinvertebrates entrained in the water column during the floods ranged from $\sim 33 \times 10^6$ individuals (August 2001) to $>300 \times 10^6$ individuals (July 2001) (Table 1). Most drifting invertebrates were Chironomidae (53–84%), and the remaining organisms were Gammaridae (7–26%), Simuliidae (2–6%), Ephemeroptera (1–6%), and Plecoptera (1–10%).

Benthic macroinvertebrates deposited and stranded in riparian areas during floods

Lateral patterns.—The average number of benthic organisms deposited during each flood ranged from <1000 to >6000 ind./m². Densities varied substantially among lateral sampling locations during each flood (indicated by the error bars in Fig. 4) and, thus, no spatial pattern was evident (data not shown).

Temporal patterns.—No temporal pattern was evident in the number of benthic macroinvertebrates deposited in the flooded riparian area during each flood (Fig. 4). For example, significantly large peaks in benthic deposition occurred late in the flood in June 2001 (1500 h), early in the flood in July 2001 (0915 h), and mid-way through the flood in August 2001 (1330 h) (Tukey's test, $p < 0.05$).

The densities of stranded macroinvertebrates collected from isolated bodies of standing water in the riparian area immediately following each flood ranged from >6000 /m² (June and August 2001) to 22,000/m² (July 2001).

Habitat-specific response of macroinvertebrates to flooding

Mean water velocity was slowest in pools (0.23 m/s) and fastest in the riffle (0.55 m/s).

Mean substratum size ($n = 50$ per habitat type, b-axis) decreased in habitats in the order, bedrock $>$ riffle $>$ run $>$ pool, and ranged from 26-cm cobble in the riffle to sand/gravel in the pools. Channel slope was $<1\%$ in all habitat types except the riffle (4%). Depth ranged from 16 cm (riffle) to 46 cm (pool), and habitat width ranged from 10 m (bedrock) to 17 m (pool and riffle).

Different habitat types supported different assemblages of benthic macroinvertebrate before the floods (Table 2). Mean proportional representation of Chironomidae was very high in bedrock habitats ($>91\%$), but it was significantly lower in the pools and runs (65 and 55%, respectively) (ANOVA, $p = 0.007$). In contrast, mean proportional representation of Gammaridae was significantly higher in pools (21%) and runs (19%) than in bedrock and riffle habitats (0–3%) (ANOVA, $p < 0.0001$). Mean proportional representation of Simuliidae was significantly higher in the riffle (18%) than in any other habitat types, where they made up $<1\%$ of the assemblages (ANOVA, $p = 0.018$). Mean proportional representation of Plecoptera was significantly higher in runs (12%) than in other habitat types (ANOVA, $p = 0.020$). Other groups (mostly other dipterans and the turbellarian *Crenobia alpina*) averaged 2 to 9% of the assemblages in all habitats before the floods, although they comprised 11 to 27% of assemblages before the last flood in August 2002 (Table 2).

The mean proportional representation of most taxonomic groups was highly variable within habitat types before and after the floods, and average assemblage composition

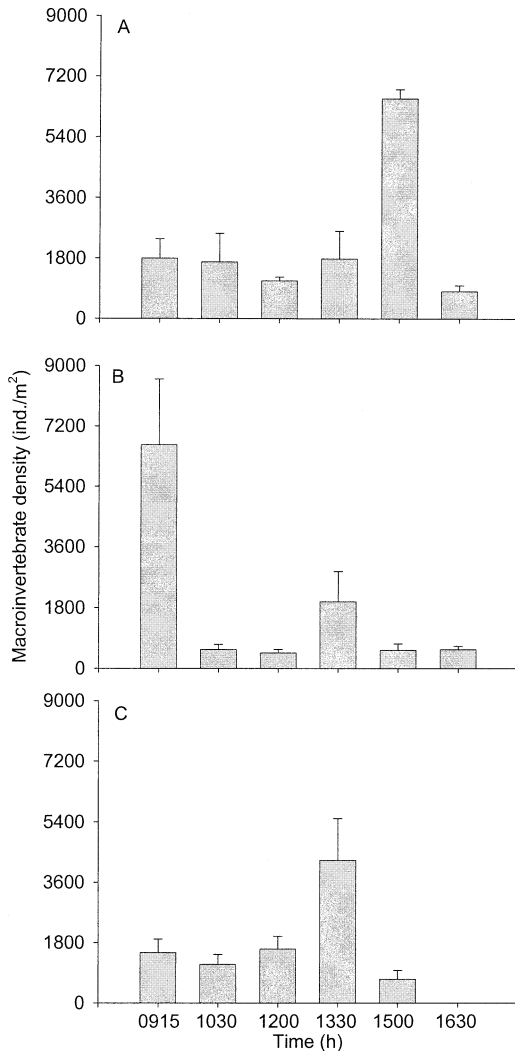


FIG. 4. Mean (+1 SD) density of benthic macroinvertebrates collected across the inundated channel during 3 experimental floods in 2001. A.—June 2001 (average peak flow: 12 m³/s). B.—July 2001 (31 m³/s). C.—August 2001 (12 m³/s). Sample collection began 30 min after peak flow was reached in each flood (i.e., 0915 h). Sample means were calculated across all lateral sampling stations for each time ($n = 3$).

changed little after the floods (Table 2). However, major redistributions in some taxonomic groups occurred in response to floods (Table 3). The proportional representation of Chironomidae decreased after floods, although they remained the most common group in all habitat types. The proportional representation of

Gammaridae was similar before and after the floods in 2001, but decreased substantially in pools and runs following the first flood in 2002 (Table 2). The average proportional representation of Ephemeroptera (mostly *Baetis* spp.) increased in all habitat types following each flood, although decreases occurred following some individual floods in the run habitat (Table 2). In 2002, the turbellarian *Crenobia alpina* became a major component of the assemblage in pools and runs.

Total macroinvertebrate density was significantly affected by the flood \times habitat type interaction (3-way ANOVA, $p = 0.0017$) and the habitat type \times before/after interaction (3-way ANOVA, $p < 0.0001$), but not by the interaction of flood \times habitat type \times before/after (3-way ANOVA, $p = 0.109$) (Table 3). Proportional representation of Gammaridae, Simuliidae, and Plecoptera was significantly affected by the 3-way interaction ($p < 0.001$) (Table 3). For these groups, the effect of the first flood was significantly different from that of later floods (Tukey's test, $p < 0.05$), and the responses of each group reflected differences in proportional representation in different habitat types (Table 2). In contrast, the proportional representation of Chironomidae and Ephemeroptera was not affected by the 3-way interaction ($p = 0.18, 0.59$, respectively) (Table 3). The proportional representation of Chironomidae was high in all habitat types; thus, Chironomidae responses were similar to those of total macroinvertebrate densities (see below). Ephemeroptera were affected negatively by the first flood (Tukey's test, $p < 0.05$), but their proportional representation increased after later floods and over time (Table 2).

The relative loss/gain of macroinvertebrates after flooding differed among the 4 habitat types and 5 floods (Fig. 5). In general, bedrock habitats lost fewer macroinvertebrates than other habitat types (~40%), whereas pools, runs, and riffles showed similar, and relatively high, losses (>80%) after the floods. Proportionally fewer macroinvertebrates were lost during the later floods in each year (Tukey's test, $p < 0.05$), particularly in August 2001 and in bedrock and riffles after the August 2002 flood (Fig. 5). In fact, macroinvertebrate density increased in riffles after the low magnitude flood (10 m³/s) in August 2001.

TABLE 2. Proportional representation (%) of common taxonomic groups in 4 habitat types before and after 5 experimental floods and across all floods. Other = Diptera that were not Simuliidae or Chironomidae and the turbellarian *Crenobia alpina*. $n = 10$ samples collected before and after each flood in each habitat type for individual floods. Numbers in parentheses are SD calculated across 5 floods. See text for peak discharges of each flood.

	June 2001		July 2001		August 2001		July 2002		August 2002		Combined	
	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
Pool												
Chironomidae	62	64	58	43	70	62	67	40	70	55	65 (5)	53 (11)
Gammaridae	31	10	26	37	17	21	29	1	0	1	21 (13)	14 (15)
Simuliidae	0	7	0	0	0	5	0	0	2	6	0 (1)	4 (3)
Ephemeroptera	0	11	1	5	0	10	0	13	1	3	0 (1)	8 (4)
Plecoptera	4	4	7	3	6	0	3	0	0	0	4 (3)	1 (2)
Other	3	4	8	12	7	2	1	46	27	36	9 (10)	20 (20)
Run												
Chironomidae	42	44	44	23	78	70	51	42	59	32	55 (15)	42 (18)
Gammaridae	27	34	29	31	9	16	28	3	0	2	19 (13)	17 (15)
Simuliidae	0	3	0	9	0	3	0	0	7	13	1 (3)	6 (5)
Ephemeroptera	7	4	12	17	4	2	5	12	7	3	7 (3)	8 (7)
Plecoptera	25	13	13	7	5	1	15	0	0	0	12 (10)	4 (6)
Other	0	0	2	13	4	8	1	43	27	50	7 (11)	23 (22)
Bedrock												
Chironomidae	97	90	93	71	97	96	89	57	82	73	92 (6)	77 (16)
Gammaridae	1	0	1	2	0	1	0	3	0	0	0 (1)	1 (1)
Simuliidae	0	1	0	0	0	1	1	6	5	10	1 (2)	4 (4)
Ephemeroptera	2	7	3	24	1	1	8	24	2	1	3 (3)	11 (12)
Plecoptera	1	1	3	2	1	0	0	9	0	0	1 (1)	2 (4)
Other	0	0	0	1	1	1	2	1	11	15	3 (5)	4 (6)
Riffle												
Chironomidae	89	69	65	44	100	90	91	77	45	46	78 (23)	65 (20)
Gammaridae	0	3	0	0	0	2	0	0	0	0	0 (0)	1 (1)
Simuliidae	11	18	35	32	0	6	3	7	39	36	18 (18)	20 (14)
Ephemeroptera	1	15	0	15	0	2	6	3	0	0	1 (3)	7 (7)
Plecoptera	0	4	0	3	0	0	0	0	4	0	1 (2)	1 (2)
Other	0	0	0	6	0	0	0	13	12	18	2 (5)	7 (8)

TABLE 3. F -values for effects of flood (F), habitat type (H), and time (T) (before/after flooding) on total benthic densities, and densities of Chironomidae, Gammaridae, Simuliidae, Ephemeroptera, and Plecoptera. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Effect	Total density	Chironomidae	Gammaridae	Simuliidae	Ephemeroptera	Plecoptera
F	380.74***	296.25***	59.60***	36.59***	24.43***	51.53***
H	45.87***	47.11***	127.94***	30.97***	22.31***	65.58***
T	299.72***	268.78***	53.63***	1.26	0.02	41.45***
F × H	2.69**	3.26***	9.05***	7.48***	1.88*	11.82***
F × T	20.14***	16.73***	4.66**	2.08	4.42*	1.18
H × T	16.69***	12.28***	27.71***	9.52***	7.46***	20.22***
T × H × F	1.53	1.36	5.07***	3.39***	0.85	3.14***

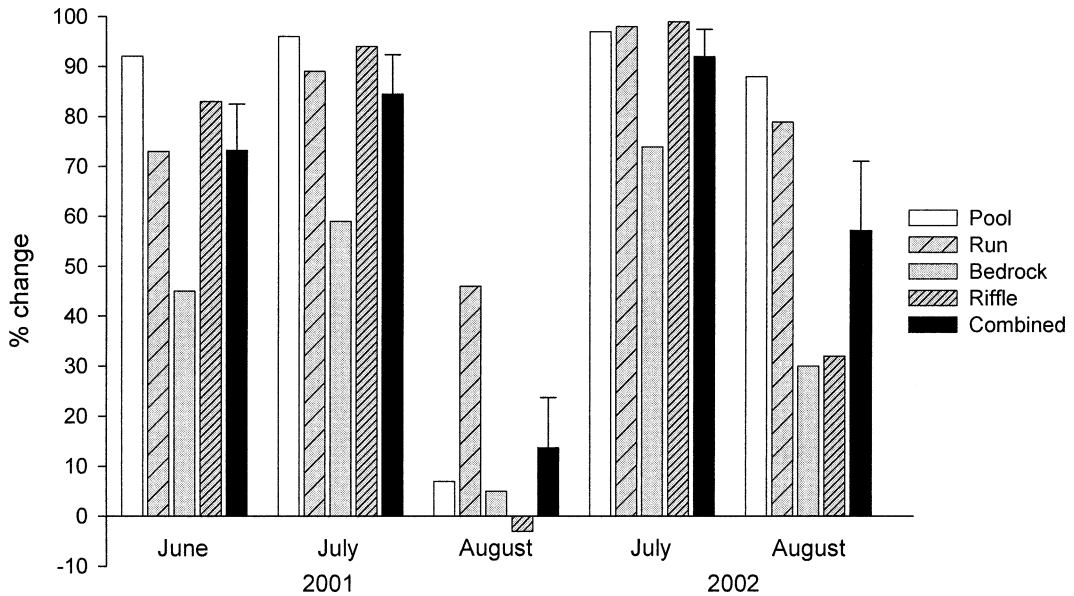


FIG. 5. Mean % change in macroinvertebrate density in pool, run, bedrock, and riffle habitats ($n = 10$ for each habitat type), and mean % change ($+1$ SE) in macroinvertebrate density for all habitats combined in the Spöl River following 5 floods in 2001 and 2002. Values <0 indicate a net gain of individuals in a habitat, values >0 indicate a net loss of individuals from a habitat.

Discussion

Seston, drift, and benthic macroinvertebrates during floods

Lateral patterns.—Our results indicated substantial amounts of seston and macroinvertebrate drift in the inundated riparian area during each flood. Matthaei and Townsend (2000) also observed that a large number of macroinvertebrates were deposited in inundated floodplain gravels during floods. This type of accumulation of seston and macroinvertebrates presumably is caused by physically passive movements of particles in response to changes in current velocity in the channel. High velocities in midchannel push particles outward into the lateral margins of the stream, where slow flows allow light particles to settle (Vogel 1981, Hart and Finelli 1999). Slow velocities along the lateral margins of the stream also should allow drifting macroinvertebrates to use behavioral adaptations such as swimming or body positioning to settle to the stream bottom more rapidly than they would by passive deposition (Ciborowski and Clifford 1983, Imbert and Perry 2000). Re-entrainment of macroinvertebrates and particles is

probably less likely in lateral margins, where flows are slower than in midchannel.

However, lateral patterns in the drift and deposition of benthic macroinvertebrates were not observed during most floods. The relatively passive action described above may explain the lack of lateral patterns in macroinvertebrate drift and deposition. Moreover, temporal patterns in the deposition of macroinvertebrates in lateral margins were not consistent among floods. Thus, lateral margins did not appear to function as refugia from flood flows in our system. These results were in contrast to those of Rempel et al. (1999) who found lateral differences in the abundance of macroinvertebrates with changing stage. However, the part of the river in which Rempel et al. (1999) worked was not confined by canyon walls and had a natural hydrograph (i.e., natural floods were studied).

Higher macroinvertebrate densities were observed on riparian substrata with grass than on sand or gravel (CTR, personal observation), suggesting that patches of vegetation may act as filters that collect organisms, or that organisms settle and remain in these vegetated patches. Palmer et al. (1995, 1996) also found patch-spe-

cific effects on macroinvertebrates during floods; flow-sheltered patches accumulated organisms, whereas nonsheltered patches did not. Our results suggest that riparian vegetation in flooded floodplains may influence the lateral distribution and deposition of invertebrates during floods.

Benthic macroinvertebrate densities in the inundated riparian area during each flood ranged from hundreds to thousands per m², similar to benthic densities in the river before the floods. (However, densities relative to total area were clearly different between the 2 habitats.) Many of the organisms in the inundated riparian area return to the main channel as flood waters recede (Prévot and Prévot 1986, Badri et al. 1987, Matthaei and Townsend 2000), but a substantial number become stranded in isolated bodies of standing water. In our study, up to 22,000 ind./m² became stranded after the floods, and Perry and Perry (1986) found 50,000 to 100,000 ind./m² stranded following floods. Stranded organisms can represent a high % of the invertebrates present in a system, and stranding can be a major source of mortality following floods. In a New Zealand floodplain river, 83% of the organisms that drifted into the lateral margins became stranded (Matthaei and Townsend 2000). Our results and those of others raise the question: given the high risk of stranding, are riparian areas flow refugia for macroinvertebrates during floods? Collectively, these findings suggest that the potential for habitats to act as flow refugia in streams is a function of complex factors and should be better related to the spatial dynamics of flow forces during floods.

Temporal patterns.—Mean peak macroinvertebrate drift densities during the floods ranged from 250 to ~1300 ind./m³, resulting in a total of 33×10^6 to $>300 \times 10^6$ macroinvertebrates drifting during the course of a flood. Perry and Perry (1986) observed drift densities that were as high as 3000 ind./m³ with $>100 \times 10^6$ benthic invertebrates being entrained. Chironomidae made up the greatest % of drift during each flood and appeared prone to drift as soon as flooding began (also see Gayraud et al. 2000, Imbert and Perry 2000). Other taxa may have behaviors that enable them to escape flood disturbance. For example, Holomuzki and Biggs (1999, 2000) found that a stream-dwelling snail (*Potamopyrgus*), a mayfly (*Deleatidium*), and caddisfly (*Pycnocentroides*) moved to slow-velocity

areas, and Hart and Finelli (1999) observed simuliids moving to protected areas as flows increased. In contrast, most of the common benthic macroinvertebrates in our stream drifted during the floods, suggesting a passive and immediate drift response. This difference in tendency to drift between organisms in our study system and in others may simply indicate that the assemblage composition of the Spöl River had yet to change in response to the new flow conditions, and consisted of taxa still adapted to stable and constant flows. For instance, Robinson et al. (2003b) documented a shift in assemblage composition after 3 y of the experimental flood program that appears to be a response to the new flow regime. Whether this compositional shift will be reflected in different drift patterns during future experimental floods remains to be tested.

Both seston AFDM and macroinvertebrate density in the drift increased rapidly when flow increased, peaked within the first few hours of each flood, and declined to near baseflow values within 3 to 5 h of the start of each flood. This temporal pattern is similar to the typical hysteresis response observed in other studies (e.g., Lenzi and Marchi 2000). Perry and Perry (1986) reported that drift increased exponentially during the initial phases of bed-moving floods (also see Gayraud et al. 2000). Further, Imbert and Perry (2000) observed increases in drift even during nonscouring, high-flow events, although a stepwise increase in flow resulted in a delayed peak increase in drift. The similar hysteresis pattern observed in seston AFDM and macroinvertebrate drift among the different floods suggests that flood magnitude, rather than duration, plays a more important role in the initial redistribution of macroinvertebrates from floods in canyon-confined rivers. For instance, the number of entrained macroinvertebrates was 3 to 10× greater during the large-magnitude floods than the small-magnitude floods.

A secondary peak in seston AFDM was observed during one of the major floods (July 2001) in our study, and that peak probably resulted from side-slope failure that caused an abrupt input of sediments; a similar secondary peak was not observed in the density of macroinvertebrates in the drift. The Spöl River flows through a confined canyon downstream of the dam, and talus fields abut the channel at many

points. These talus fields were scoured severely by the floods (Mürle et al. 2003).

Habitat-specific responses of macroinvertebrates to floods

The floods reduced instream, benthic densities of macroinvertebrates by 14 to 92%, depending on flood magnitude. Floods often cause substantial decreases in macroinvertebrate densities (Grimm and Fisher 1989, Giller et al. 1991, Cobb et al. 1992, Maier 2001). However, our results also indicated habitat-specific responses of macroinvertebrates to flood disturbance. Invertebrates in bedrock areas appeared to have the highest resistance to floods, whereas those in pools and runs showed the lowest resistance. Bedrock is more physically stable than substrata in pools (sand and gravel) and runs (gravel and cobble), and pools are heavily scoured during flood disturbance (Lytle 2000). Matthaei and Huber (2002) showed that microform bed clusters (rocks associated with a large stable boulder in a stream) acted as refugia during floods. Further, different stream habitats harbor different species in different relative proportions (Angradi 1996). Thus, differential responses to flood disturbance are expected among assemblages in different habitats (e.g., Armitage and Gunn 1996).

Habitat-specific responses of assemblages to floods also differed among floods. For example, the loss of organisms was substantially lower in the 3rd (August 2001) and the last (August 2002) small floods than in previous floods. These results suggest that evaluations of the effects of flood disturbances should be placed in the context of the timing and magnitude of previous floods (see Death 1996) because present assemblage composition reflects disturbance impact of and recovery dynamics from previous floods. Thus, present assemblage composition can influence the disturbance impact of the current flood. However, large floods will have pronounced effects on assemblage composition and abundance regardless of antecedent flood history. The larger floods in July 2001 and 2002 reduced benthic abundances to a much larger extent than the smaller floods.

Our results indicated a temporal pattern of change in the susceptibility of the macroinvertebrate assemblage to flood disturbance after sequential floods. Chironomidae are a dominant

group in the drift during floods (Perry and Perry 1986, Imbert and Perry 2000). More Chironomidae were lost from all habitats in later floods than in earlier floods. This pattern may have been related to the compositional shifts in the assemblage. Gammaridae became less abundant, whereas Chironomidae and Simuliidae became more abundant in the Spöl River between 1999 and 2002 (Robinson et al. 2003b). Thus, as the species composition shifts in response to the new flow regime in the Spöl River, the response of the macroinvertebrate assemblage to flood disturbance also should shift to reflect associated changes in biotic properties and resilience of the assemblage.

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