Post-Flood Recovery of a Macroinvertebrate Community in a Regulated River: Resilience of an Anthropogenically Altered Ecosystem

Russell B. Rader,^{1,2} Neal J. Voelz,³ and James V. Ward^{4,5}

Abstract

Preservation of biodiversity depends on restoring the full range of historic environmental variation to which organisms have evolved, including natural disturbances. Lotic ecosystems have been fragmented by dams causing a reduction in natural levels of environmental variation (flow and temperature) and consequently a reduction of biodiversity in downstream communities. We conducted a long-term study of the macroinvertebrate communities before and after natural flood disturbances in an unregulated reference site (natural flows and temperatures), a regulated site (regulated flows and temperatures), and a partially regulated reference site (regulated flows and natural temperatures) on the upper Colorado River downstream from a deep-release storage reservoir. We aimed to test the hypothesis that floods and temperature restoration would cause an increase in macroinvertebrate diversity at the regulated site. Over the short term, macro-

Introduction

Preservation of biodiversity depends on maintaining the full range of historic environmental variation (especially disturbances) to which organisms have evolved (Paine et al. 1998; Gunderson et al. 2002). Humans often cause a reduction in biodiversity by reducing and/or altering natural patterns of environmental variation (Pickett & White 1985; Camargo 1998; Poff & Ward 1990). When key factors are altered by human intervention, communities can shift states to lower diversity and alternative community compositions because species often lack the evolutionary mechanisms to respond to human alterations (e.g., Gunderson et al. 2002; Folke et al. 2004). Community stability measures the relative constancy of species abundances over time in the face of disturbance and has two components

Address correspondence to: R. B. Rader, email russell_rader@byu.edu ³ Department of Biological Sciences/MSB 262, St. Cloud State University, St. Cloud, MN 56301, U.S.A.

⁵ Present address: 2298 Todd Street, Eugene, OR 97405, U.S.A. The order of the first two authors was decided by a coin toss.

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invertebrate richness decreased at the regulated site when compared to pre-flood levels, whereas total macroinvertebrate density remained unchanged. Over the long term (1 and 10 years after the floods), macroinvertebrate diversity and community structure at the regulated site returned to pre-flood levels without increasing to reference conditions. Occasional floods did not restore biodiversity in this system. As long as the physical state variables remain altered beyond a threshold, the community will return to its altered regulated condition. However, temperature restoration at the partially regulated site resulted in an increase in macroinvertebrate diversity. Our results indicate that restoration of the natural temperature regime will have a stronger effect on restoring biodiversity than occasional channel-forming floods.

Key words: floods, macroinvertebrate diversity, stream regulation, stream restoration, temperature restoration.

(e.g., Holling 1973; Connell & Sousa 1983). The first component is resistance and involves the ability of an assemblage to remain unchanged by disturbances. The second is resilience, which is the return of a community to predisturbance conditions (e.g., Holling 1973; Gunderson et al. 2002). Recovery is a general term that describes the change in community structure following a disturbance, which may include resiliency or changes to a new alternative stable state (e.g., Gunderson et al. 2002).

Most lotic networks have been fragmented by dams that disrupt the river continuum, alter key factors (e.g., temperature), and reduce natural levels of environmental variation causing downstream communities to shift to an alternate state (e.g., Petts 1984; Dynesius & Nilsson 1994; Stanford et al. 1996; Ward 1998). Regulated rivers downstream from deep-release reservoirs used for water storage show a reduction in macroinvertebrate diversity compared to unregulated conditions because of reduced daily, seasonal, and annual variation in temperature and flow (e.g., Petts 1984; Ward 1998).

Recent conservation efforts have emphasized restoring natural patterns of variation in key factors to increase diversity in regulated rivers (Stanford et al. 1996; Poff et al. 1997). For example, macroinvertebrate diversity and biomass increased 2 months after a large test flood in the

¹ Department of Integrative Biology, Brigham Young University, 401 WIDB, Provo, UT 84602, U.S.A.

Department of Limnology, EAWAG/ETH, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland

middle Colorado River below Glen Canyon Dam (Shannon et al. 2001), and there were some beneficial effects of implemented floods on macroinvertebrate community structure in a Swiss river (Robinson et al. 2003; Jakob et al. 2003). These results are consistent with the hypothesis that restoring some degree of natural variation can cause an increase in diversity in stream communities altered by human intervention (e.g., Stanford et al. 1996; Poff et al. 1997). However, diversity can also remain unchanged as a result of restoration. For example, partial recovery of the thermal regime downstream from a dam did not cause an increase in macroinvertebrate richness or a change in species composition (e.g., Vinson 2001). Ecosystems altered by human intervention may not respond to restoration if we fail to restore key components of the full range of variation in factors that sustained historic levels of diversity.

Most studies on stream restoration have been relatively short term. That is, recovery is rarely studied for longer than 1 year following a disturbance. Long-term studies are needed because they can better distinguish the end-point of recovery from transitory stages (Niemi et al. 1990; Voelz et al. 2000). It may take years to determine the response of an altered community to restoration depending on the life history characteristics of the recovering species (e.g., rates of dispersal). We followed previous precedence and defined "long term" as at least two generations of the species with the longest generation time (e.g., Jackson & Füreder 2006). None of the macroinvertebrate species in our study had a generation time longer than 2 years. Thus, at least 4 years would be necessary to determine the long-term pattern of recovery in this study.

We conducted a long-term study of a macroinvertebrate community altered by human intervention following a natural disturbance in a regulated section of the upper Colorado River. We hypothesized that macroinvertebrate diversity would increase following two consecutive floods in 1983 and 1984. To test this hypothesis we measured macroinvertebrate richness, community composition, and total density in an unregulated reference site (Ref 1), a regulated site (Reg), and a partially regulated site (Ref 2) for multiple years prior to the floods, shortly after both floods, and 1 and 10 years following the second flood. The unregulated reference site was 5 km upstream from the dam, whereas the regulated site and partially regulated site (regulated flows, but near-natural temperatures) were 400 m and 5 km downstream from the dam, respectively. An increase in richness and community similarity (species composition and total density) between the regulated site (Reg_{postflood}) and the reference sites (Ref $1 = \text{Ref } 2 = \text{Reg}_{\text{postflood}} >$ Reg_{preflood}) at any of the two points during recovery (shortly after and 1 year) and following recovery (10 years) would indicate a positive effect of floods in restoring the macroinvertebrate community at the regulated site. However, the absence of an increase in diversity and similarity or lower diversity during or following recovery at the regulated site (Ref $1 = \text{Ref } 2 > \text{Reg}_{\text{preflood}} \ge \text{Reg}_{\text{postflood}}$) would indicate the ineffectiveness of floods in restoring the macroinvertebrate community and thus a lack of resiliency. We measured changes in macroinvertebrate habitat (e.g., mosscovered rocks), macroinvertebrate food resources, and physical/chemical factors at the regulated site before and after both floods to better understand the mechanisms causing the response of macroinvertebrates to the flood disturbances.

We also hypothesized that restoring the natural temperature regime would have a positive effect on restoring macroinvertebrate diversity downstream from this deeprelease storage reservoir. To test this hypothesis we compared macroinvertebrate diversity and similarity in community composition in the pre-flood, regulated site (Reg_{preflood}) to Ref 1 with natural flows and temperatures and Ref 2 with regulated flows but near-normal, unregulated temperatures. Greater similarity in diversity and community composition between the reference sites than between the reference sites and the pre-flood, regulated site would indicate a positive effect of restoring the temperature regime on restoring macroinvertebrate diversity (Ref $1 = \text{Ref } 2 > \text{Reg}_{\text{preflood}}$). Alternatively, greater similarity in diversity and community composition between Ref 2 and Reg_{preflood} would indicate that restoration of the temperature regime would have no effect on restoring diversity (Ref $1 > \text{Ref } 2 = \text{Reg}_{\text{preflood}}$).

Site Descriptions

Granby Reservoir (lat 40°11'N, long 105°52'W) began operation on the upper Colorado River in September 1949. It is a deep-release storage impoundment with a dam 91 m high. The river at this point drains a sixth-order basin with an area of approximately 810 km². Previous studies have compared macroinvertebrates in an unregulated reference site in Rocky Mountain National Park to macroinvertebrates in sites located along a recovery gradient downstream from the reservoir (Rader & Ward 1988; Voelz & Ward 1991). We collected long-term data on macroinvertebrates before and after two floods in a single riffle circa 400 m from the dam in a regulated zone. The regulated zone (2,460 m above sea level) extends circa 0.75 km from the dam and is characterized by both regulated flows and altered temperatures (summer cool and winter warm), whereas the recovery zone (approximately 0.75-10.0 km downstream from the dam) is characterized by regulated flows and recovered temperatures similar to the unregulated reference site.

Long-term flow records were obtained from U.S. Geological Survey gauging stations, which included a site approximately 300 m downstream from Granby Reservoir. Average annual discharge prior to regulation (8.7 m^3 /second) was six times greater than average discharge following regulation (1.5 m^3 /second; Fig. 1). Regulated flows before and after the 1983 and 1984 floods showed a constant pattern that peaked at about 2.3 m³/ second in July, decreased to about 1.1 m³/second during



Figure 1. Flow before and after regulation. Construction of the dam is indicated by a dashed arrow, whereas solid arrows indicate macroinvertebrate sampling periods.

August, and remain at approximately 0.6 m³/second from September through April. This pattern has been maintained in 37 out 44 years since the dam was constructed (Fig. 1).

Although we have no temperature data prior to dam construction, comparisons between regulated and unregulated conditions (1981-1982), downstream and upstream from the dam, respectively, were consistent and reflected typical conditions downstream from other deep-release reservoirs from around the world (Rader & Ward 1988; Voelz & Ward 1991). The regulated and recovery sites (Reg and Ref 2) had a greater number of annual degree days (the thermal energy available for growth and reproduction) than the unregulated site (Ref 1) because of winter warm conditions (Table 1). The unregulated reference site was covered with ice and had freezing water temperatures (0°C) for 5-6 months, whereas the regulated zone never dropped below 2°C. The recovery site (Ref 2) was partially frozen for 2 or 3 months at temperatures of 0°C. Also, the annual coefficient of variation at the unregulated site was over two times greater than the regulated site because summer cool temperatures reduced both daily and seasonal variation at the regulated site (Table 1).

Table 1. Temperature characteristics at the unregulated reference site upstream from the dam (Ref 1), the regulated site (Reg), and the partially regulated, downstream reference site (Ref 2).

Sites	Elevation (meters above sea level)	Annual Degree Days (°C)	CV (%)	Maximum (°C)	Minimum (°C)
Ref 1	2,590	1,330	119	18.0	0.0
Reg	2,450	1,729	53	9.8	2.0
Ref 2	2,426	2,082	64	18.2	0.0

CV, coefficient of variation.

Water chemistry and riparian vegetation were similar between the regulated (Reg), unregulated (Ref 1), and recovery sections (Ref 2). Dissolved oxygen was always high usually near 100% saturation, NO₃-N concentrations were less than or equal to 0.07 mg/L, and total hardness ranged from 18 to 24 mg/L. pH was circumneutral but tended to increase (daytime) and decrease (nighttime) on a diel basis. Although the benthic substrate primarily consisted of cobble, pebble, and gravel at each site, there was a greater proportion of boulders downstream from the dam (Reg and Ref 2) than upstream (Ref 1). Willows (*Salix* spp.) were the dominant riparian vegetation at all sites (Rader & Ward 1988; Voelz & Ward 1991). Detailed descriptions of each site can be found in Rader (1987), Rader and Ward (1988), Voelz (1990), and Voelz and Ward (1991).

Background

On rare occasions, heavy spring rain can coincide with heavy snow-pack run-off, and water levels may exceed the capacity of the reservoir making it necessary to discharge excess water downstream. Such a situation occurred during 1983 and 1984 in the Colorado River below Granby Reservoir setting the stage for a natural experiment on the response of the macroinvertebrate community to two consecutive floods. For 2 consecutive years, regulated hypolimnetic flows became unregulated epilimnetic flows that spilled over the top of the dam. We considered these floods to be natural disturbances because they were produced by natural processes (e.g., spring snowmelt) and because the primary mechanisms causing the displacement of benthic macroinvertebrates (shear stress and bed movement) were the same as natural spring floods in unregulated streams (Bond & Downes 2000; Death 2002).

Peak flows during 1983 and 1984 were approximately 2.5 times greater than the estimated discharge (29.8 m³/second) required to transport the mean substrate particle diameter (8.5 cm) in the regulated site downstream from the dam (Rader & Ward 1988). This flow had not been attained at the regulated site in the 32 years since the dam was constructed (Fig. 1).

During the flood of 1983 the hydrograph downstream from the reservoir rose to 6.1 m³/second on July 1, approximately 2.5 times greater than the previous day. It reached a maximum of 69.7 m³/second on July 12 and decreased to normal regulated flows by 11 August. This was a relatively short event compared to the flood of 1984, which began in late March (27.3–36.8 m³/second), reached a peak in mid-July (59.7 m³/second), and did not subside until the first of August (1.1 m³/second). The flood of 1984 increased gradually over a much longer time than the flood of 1983. Water was released from the epilimnion of the reservoir during both floods causing downstream temperatures to increase from 5–9°C to 12–15°C.

Methods

Macroinvertebrate samples and physical/chemical data were collected at the regulated site (Reg) during 1978-1979 (Ward, unpublished data), 1982–1983 (Rader 1987; Rader & Ward 1988), 1984-1985 (Voelz 1990; Voelz & Ward 1991), and 1993–1994 (Rader, unpublished data). Samples for three of these five studies were collected monthly for an entire year (1978-1979, 1982-1983, and 1984-1985). However, we only compared samples collected from the same months before (1978, 1982, 1983) and after flooding (1983, 1984, 1985, and 1993–1994) in order to document recovery in the macroinvertebrate assemblage without bias associated with comparing different seasons across years. In 1983 and 1984, samples were collected just prior to both floods in June and March, respectively, again during the descending hydrograph (July), and monthly from August to December after flows returned to normal levels. Samples were also collected once a month for 1 year at both reference sites (Ref 1 and Ref 2) during 1982-1983, and again at Ref 2 during 1984-1985. Thus, samples at Ref 2 were collected the year before, during, and following both floods, whereas samples at Ref 1 were collected the year before and during the first flood.

Three to five macroinvertebrate samples were collected monthly with a Surber sampler $(0.09\text{-m}^2 \text{ area sampled};$ mesh = 240 µm) at each site except 1984–1985. During 1984–1985, four samples were collected per month by removing invertebrates with a hand net (240-µm mesh) from a metal core (0.05 m^2) . Data from these two samplers were comparable because they enclosed a similar area, had the same mesh size, and were only used to compute the relative abundance of invertebrates. Different sampling devices, which were very similar in this study, have a much smaller effect on estimates of relative abundance than estimates of absolute abundance (e.g., Rader & Shiozawa 2001). Samples were also processed in a similar manner in the laboratory for each study (Rader 1987; Rader & Ward 1988; Voelz 1990; Voelz & Ward 1991). They were rinsed through nested sieves with 1-mm and 250- μ m openings, and the greater than 1-mm fraction was completely sorted. The 250- μ m to 1-mm portion was either completely sorted or subsampled and sorted by one-half or one-quarter. Macroinvertebrates were identified to the lowest feasible taxonomic level except Acarina, Chironomidae, and Oligochaeta. A few taxa from the reservoir (e.g., *Mysis relicta*) were eliminated from our analysis because they did not maintain viable populations in the river.

Comparisons of macroinvertebrate richness across time at the regulated site and between the regulated site and the reference sites may be biased by the number of individuals in a sample and the total area sampled, which will affect the probability of encountering a given taxon (James & Rathbun 1981; McCabe & Gotelli 2000). Richness was rarefied for differences in the number of individuals collected and area sampled for all years and sites (EcoSim version 7.7; Gotelli & Entsminger 2004). Rarefied richness in samples with the greatest abundance was reduced to the level of samples with the least abundance. Default values in EcoSim were used for all analyses (e.g., 1,000 iterations). We used a permutation test to determine significant differences (p < 0.05) between times and sites (Gotelli & Entsminger 2004).

Kendall's coefficient of concordance (*W*) was used to determine changes in the rank order of just the dominant species before and after each flood at the regulated site. This analysis provided partial insight into how community composition changed following the floods in order to test the first hypothesis. Kendall's *W* was calculated (SPSS 11.5 for Windows) using average densities of the 12 dominant taxa for the same 5 months (July to October and December) for each year (1978, 1982, 1983, 1984, 1985, 1993).

We also used nonmetric multidimensional scaling (NMDS) to further examine changes in macroinvertebrate species composition using all taxa collected at each site before and after both floods at the regulated site and between the regulated site and the reference sites (Legendre & Legendre 1998). NMDS can simultaneously compare communities across space and time. We used data collected during June to October, December, and March for all years because these months allowed a longer temporal view of assemblage dynamics before and after flooding. The ordinations were run using logarithmically transformed abundance data (log_e X+1). NMDS was obtained using PCord and Sørensen's index of community similarity (McCune & Mefford 1999). Sørensen's index gives less weight to outliers and is the recommended distance measure for NMDS (McCune & Mefford 1999). The NMDS autopilot mode was set at medium (maximum iterations = 200), which recommended a two-dimensional solution with a final stress value of 12.8. Although multivariate statistical analyses cannot test hypotheses, that is the role of permutation procedures.

We used multiresponse permutation procedures (MRPP) to test for pair-wise differences in community composition between years at the regulated site and between the regulated site and the reference sites. MRPP is a nonparametric, distance-based procedure that measures the extent to which two communities overlap based on the observed compared to the permutated average within-group distance among samples (Biondini et al. 1991; Mielke & Berry 2001). This statistic ranges from -1to 1, with values larger than 0 indicating differences in community composition that are greater than expected by chance (p < 0.05). Distances were based on Sørensen's (Bray-Curtis) coefficient of similarity, which was rank transformed to correct for a loss of sensitivity attributed to heterogeneous data (McCune & Grace 2002). All MRPP tests were conducted using PC-ORD Version 4.36 (McCune & Mefford 1999).

Mineral substratum samples and sedimentary detritus were compared the year before (1982) versus the year following (1985) the floods of 1983–1984 at the regulated site. Mineral and detritus samples were collected separately using a steel core (28-cm diameter) driven 15 cm into the substrate. All sediment and water were removed from mineral samples using a hand-operated pump and dry sieved into size categories based on Cummin's modification of the Wentworth scale. For detritus samples, all substrate materials were vigorously stirred and larger particles were removed with a small hand-held net (1-mm mesh). Fine particles in suspension were sieved (15 L) through a 240-µm mesh, whereas two 1-L subsamples were collected to determine the mass of remaining particles (<240 µm). Each detrital size fraction was dried to a constant weight, combusted, and weighed in the laboratory (Rader & Ward 1988; Voelz & Ward 1991). The percent cover of moss with associated strands of filamentous green algae in 10 quadrats (1.0 m^2) randomly placed along two transects across the width of the stream in 1982 was compared to data collected from the same transects in 1985 and 1993.

Results

Flood Effects

Substrate size composition, the amount of sedimentary detritus, and the coverage of moss showed the effects of flooding at the regulated site. Mineral substrate at the regulated site in 1982 was predominantly cobble, pebble, and gravel (89.8% by weight), whereas sand and silt/clay were 8.0 and 2.2%, respectively (Rader & Ward 1988). After the floods (Autumn 1984–1985), the larger particles (cobble, pebble, and gravel) increased to 96.5%, whereas the smaller particles (sand and silt/clay) decreased to 3.4% and less than 0.1%, respectively (Voelz & Ward 1991). Also, there was approximately two to seven times more sedimentary detritus before than after the floods, and moss coverage decreased from 72 to 82% before (1982) compared to 30–50% after the floods (1985). However,

by 1993–1994 the moss had regrown to predisturbance coverage (Rader, unpublished data) thus, indicating that 10 years was a sufficient recovery time for mosses.

Neither flood had a strong effect on macroinvertebrate abundance at the regulated site. Total macroinvertebrate density at the regulated site following the first and second floods (16,615 and $48,743/m^2$, respectively) was greater than before the floods ($1982 = 11,436/m^2$). Also, macroinvertebrate total density at the regulated site a few days following the first flood ($15,530/m^2$) was only reduced by 30% compared to 2 weeks prior to the first flood ($22,230/m^2$). Total densities increased rapidly at the regulated site after the first flood subsided (August 1983) to 22,538 and $24,069/m^2$ in September and December of 1983, respectively. Total density at the regulated site after the flood of 1984 also showed a very quick recovery in that the post-flood densities ties quickly exceeded pre-flood densities.

In contrast to invertebrate density, flooding resulted in a decrease in invertebrate richness at the regulated site. Total richness at the regulated site was lowest following the first flood (1983) and second lowest following the second flood (Table 2). Macroinvertebrates were more resilient to the second disturbance as the total number of taxa in December 1984 (13) was almost twice that found during December 1983 (7). Richness continued to increase at the regulated site following the second flood from 13 taxa in July 1985 to 19 in September 1985. However, richness at the regulated site did not continue to increase to unregulated (Ref 1) or partially regulated (Ref 2) reference conditions (Table 2). In fact, there was no significant difference in rarefied richness at the regulated site after 10 years of recovery (1984–1985 \approx 1993–1994; Table 2; Fig. 2).

Two consecutive floods did not have a long-term effect on the relative abundance of dominant taxa at the regulated site. Rankings of the 12 dominant taxa for all sampling periods were significantly concordant, although Kendall's W was relatively low (W = 0.38, $\chi^2 = 18.4$, p = 0.001). However, Kendall's W increased (W = 0.49, $\chi^2 = 10.5$, p = 0.005) when postdisturbance data were removed from the analysis (1983 and 1984–1985). Thus,

Table 2. Observed and rarified richness for the upstream reference

 site (Ref 1), the downstream reference site (Ref 2), and the regulated

 site (Reg) across all sampling periods.*

Site and Period	Sample Size	Observed Richness	Rarefied Richness
Ref 1, 1982–1983	20	49	48.9 (47.0-48.0)
Ref 2a, 1982–1983	20	47	44.8 (43.0-44.0)
Ref 2b, 1984–1985	20	52	46.0 (43.0–50.0)
Reg pre-flood, 1978	15	31	31
Reg pre-flood, 1982–1983	20	32	27.6 (27.0–28.0)
Reg post-flood, 1983	24	12	9.7 (8.0–12.0)
Reg post-flood, 1984–1985	20	27	18.7 (15.0–22.0)
Reg recovered, 1993–1994	20	34	20.5 (17.0–22.0)

*Confidence intervals are in parentheses (95%). Observed and rarified richness were equal in 1978 because it had the lowest number of individuals.



Figure 2. Rarefaction curves showing macroinvertebrate richness standardized by area and the number of individuals collected. Ref 2a and 2b is the partially recovered site (near-natural temperatures with regulated flows) in 1982–1983 and 1984–1985, respectively. Confidence intervals are not shown for clarity.

the rank order of the dominant species at the regulated site following the floods differed from the predisturbance (1978 and 1982) and recovered (1993–1994) communities. Warmer temperatures and increased food from the reservoir (plankton) during flooding probably caused some species to temporarily increase. More importantly, ranks at the regulated site before the floods (1978 and 1982) did not differ from the recovered community (1993–1994) indicating that community structure did not change toward reference conditions following the floods.

Because it included all taxa, NMDS provided stronger evidence that the floods had no long-term effect on community composition at the regulated site. The only communities that were not significantly separated were the pre-flood communities from the regulated site (1978–1979 and 1982–1983; MRPP, A = 0.04, p = 0.18). None of the other communities significantly overlapped in ordinal space (p < 0.05). However, MRPP is a powerful test that shows separation between communities based on fairly small differences in species composition and patterns of relative abundance (e.g., Mielke & Berry 2001). Therefore, it is informative to visually examine the distance between communities in ordinal space to draw additional conclusions. In particular, the recovered community from 1993-1994 was quite close to both pre-flood regulated communities, but well separated from both reference communities (Ref 1 and Ref 2; Fig. 3). Thus, the floods did not restore community composition at the regulated site to pre-dam conditions. Plus, the 1983 post-flood community showed the effects of flooding as it was distinctly different from any other community (Fig. 3). This was not the case with the 1984 post-flood community, which was closely associated with the pre-flood community in ordinal space indicating that the first flood altered community composition more than the second flood.

The pre-flood, regulated community was dominated by Baetis mayflies, chironomids, non-insect taxa (e.g., flatworms), and Ephemerella mayflies. Ephemerella mayflies, chironomids, and some non-insect taxa decreased shortly after flooding at the regulated site, whereas simuliid blackflies increased. Simuliidae were the most abundant macroinvertebrates in postdisturbance 1983, and one of the top five most abundant taxa during 1984-1985. Simuliidae appear to thrive on disturbance conditions as they rapidly declined 3 or 4 months after each flood to 1-9% of the total invertebrate numbers. They remained at low densities through 1985 and in the 1993-1994 recovered community. Despite reductions, many of the common taxa (e.g., Baetis spp., Chironomidae) remained dominant shortly after flooding at the regulated site, as evidenced by Kendall's W (i.e., their ranked abundances remained relatively stable). The distinct separation of the post-flood 1983 community resulted from the loss of rare taxa.

Temperature Effects

Although abundances were greater, diversity was lower at the regulated site than either of the reference sites (Table 2; Fig. 2). Total macroinvertebrate density in the pre-flood, regulated site $(25,666/m^2)$ was five times greater than the pre-flood, unregulated site $(5220/m^2)$, and 1.6 times greater than the pre-flood, partially regulated site $(16,050/m^2)$. The two reference sites combined contained 16 species that were not collected at any time at the regulated site. However, richness at Ref 2 with restored temperature variation was similar to the richness at the unregulated site (Ref 1).

NMDS showed that the restored reference community (Ref 2) was different from all of the communities at the regulated site but quite close in ordination space to the unregulated reference site (Fig. 3). Thus, restoring the temperature regime can help to restore community composition. The regulated site was characterized by the absence of heptageniids mayflies, and reductions in the richness and abundance of stoneflies, caddisflies, and aquatic beetles. All three groups recovered at Ref 2, being similar in richness and abundance to the unregulated community (Ref 1). The primary difference between the unregulated and partially regulated reference sites was a greater abundance of caddisflies and non-insect taxa at Ref 2. These data suggest that restored temperatures resulted in the restoration of both macroinvertebrate community composition and macroinvertebrate richness at the partially regulated site.

Discussion

Short-Term Flood Effects

Most studies on the short-term effects of floods on macroinvertebrates in unregulated rivers show a decline in diversity and density (e.g., Molles 1985; Robinson & Minshall 1986; Boulton et al. 1988; Yount & Niemi 1990; Death 1996;



Figure 3. NMDS plot for reference sites, and pre- and post-flood communities at the regulated site. Ref 2a and 2b is the partially recovered site (near-natural temperatures with regulated flows) in 1982–1983 and 1984–1985, respectively.

Voelz et al. 2000; Maier 2001). Thus, the short-term reduction of diversity at the regulated site in our study was not surprising and was most likely caused by the displacement of rare taxa. However, the lack of a strong reduction in invertebrate densities before versus after both floods was surprising. It appears that some dominant species were resistant to the disturbance (e.g., Oligochaeta, *Baetis* spp.), whereas others (e.g., Simuliidae) quickly increased their numbers to counter the reduction in dominant species that were not resistant (e.g., chironomids and *Ephemerella* spp.).

Macroinvertebrate post-flood habitat at the regulated site shifted toward unregulated conditions as finer sediments and dense mats of moss with attached algae were flushed downstream. Smaller particles were clearly displaced, and as much as 30-40% of the benthic substrate had been moved. Moss (Fontinalis sp.) is an important habitat for many macroinvertebrates (e.g., Englund 1991; Stream Bryophyte Group 1999), and its removal may have accounted for the reduction in density of both chironomids and Ephemerella spp. following the flood of 1983 at the regulated site. Disturbance effects were reduced downstream (Ref 2) probably because of the absence of moss. Taxa that primarily used bare rock surfaces (e.g., Baetis spp.) resisted the floods and remained relatively unchanged or even increased in density. Resistant taxa may have found refuge on stable substrata during the floods and quickly recolonized open habitats from nearby boulders (Giberson & Hall 1988; Lancaster & Hildrew 1993; Matthaei et al. 1997).

Long-Term Flood Effects

Floods are part of the natural flow regime, which is one of four physical factors that determine the environmental heterogeneity for maintaining diversity in stream ecosystems (e.g., Poff et al. 1997). The other three are water chemistry, temperature, and light (e.g., Hynes 1970). Studies on the effects of river regulation support the thesis that a reduction in channel-forming floods is one of the primary causes of a decline in macroinvertebrate diversity downstream from dams (e.g., Ward 1998). Thus, we expected floods to restore the natural physical template and increase diversity following years of colonization by taxa previously excluded by regulation. That is, we predicted that the floods would increase the similarity between the regulated site and our references sites upstream or downstream from the dam. However, diversity and community composition of the 1993 macroinvertebrate assemblage after 10 years of recovery were most similar to the pre-flood, regulated assemblage.

Our results show that an occasional flood (e.g., once every 5-10 years) will do little to restore macroinvertebrate diversity in a regulated river downstream from a deep-release dam. A recent report on the long-term effects of an experimental release of high flows on the middle section of the Colorado River (Glen Canyon Dam) came to a similar conclusion (Powell 2002; Dalton 2005). The experimental flood did not cause a permanent increase in sandbars and beaches because it did not reestablish the rivers' sediment transport equilibrium. Once the floods subsided, clear water continued to erode both sandbars and beaches reversing any advantage gained by the experimental release. We suggest that it is necessary to permanently restore critical parts of the full range of both temporal and spatial variation in the factors that maintain diversity. For example, releasing part of the peak portion of the annual hydrograph each year might permanently rebuild the beaches and sandbars critical to the restoration of endangered species in the middle

Colorado River (e.g., Humpback chub [*Gila cypha*]). However, we maintain that restoring the essential aspects of the hydrograph will do little to restore macroinvertebrate diversity downstream from deep-release reservoirs without restoring other factors that also historically supported diversity.

Temperature Effects

In the regulated section of the upper Colorado River, water chemistry and light remained unaltered by the dam, whereas variation in flow and temperature were reduced (e.g., Rader & Ward 1988). We maintain that winter warm and summer cool conditions caused the reduction in macroinvertebrate diversity in the upper Colorado River following construction of Granby Dam (Rader & Ward 1988; Voelz & Ward 1991). Diversity and community composition in Ref 2 downstream from the regulated site was similar to the unregulated section (Rader & Ward 1988). Thermal diversity in the downstream reference site was nearly natural but flow was still regulated suggesting that temperature alterations more than flow accounted for the increase in diversity at Ref 2. Similarly, temperature alterations downstream from a deep-release reservoir on the Saskatchewan River resulted in a decline in diversity from 30 families and 75 species to a single family, Chironomidae (Lehmkuhl 1974). However, in the absence of a reference site with unregulated flows and regulated temperatures we cannot conclusively determine the relative importance of restoring temperatures versus flows. Nonetheless, our data show that restoring at least part of the natural temperature regime will promote diversity in regulated rivers downstream from deep-release impoundments.

Reductions in thermal diversity can decrease or increase the fitness of macroinvertebrate species depending on their specific life history adaptations (Ward & Stanford 1979; Rader & Ward 1990). Although we do not know exactly what aspect(s) of the annual temperature regime may have had the greatest impact on the reduction of diversity at the regulated site, it was clear that temperature was a critical factor (e.g., Rader & Ward 1989). For example, some species of stoneflies and mayflies that were present at our reference sites (upstream and downstream) but absent from the regulated site require 0°C during the winter and a rapid increase in temperature in the spring to break egg diapause (Harper & Hynes 1970; Ward & Stanford 1979). Temperatures rarely, if ever, drop to 0°C at the regulated site.

Three attributes characterize the thermal diversity of a stream: (1) the duration of maximum and minimum temperatures; 2) the seasonal rate of change; and 3) variation in daily fluctuations. Although the effects of more than one of these variables has rarely been considered, we know that specific aspects of the thermal regime can effect egg development (e.g., Elliott 1978), fecundity (e.g., Vannote & Sweeney 1980), dormancy (e.g., Harper & Hynes 1970), growth and maturation (Brittain 1976), voltinism (e.g., Hynes & Hynes 1975), and emergence (e.g., Lillehammer 1975). We suggest that temperature constancy is the primary factor that sets the number of species that can persist downstream from deep-release reservoirs, whereas both constant flows and temperatures allow the species that persist to reach high densities.

Implications for Stream Restoration

Key components of thermal diversity can be restored in modern reservoirs. Most modern dams (circa 1950s to the present) have been built with multiple release points spanning the entire depth of the reservoir. As such, it is possible to release water from different depths in the reservoir at appropriate times of the year to mimic aspects of the natural temperature diversity. For example, many reservoirs in colder climates (e.g., temperate zone or at higher altitudes in the tropics) are dimictic, meaning that they mix twice a year (spring and autumn) when temperatures along a depth profile are uniform at 4°C. They stratify in the summer with warm water in the upper most layers (epilimnion) and cold, dense water deep in the hypolimnion. Because freshwater is most dense at 4°C, many deep-release reservoirs in colder climates release water that is about 4°C in both the winter and the summer causing winter warm and summer cool conditions downstream from the dam. Water could be released from the upper part of the dam just below the ice during the winter to provide temperatures at or near 0°C to the downstream community to break egg diapause. Water could also be mixed from the epilimnion and the hypolimnion to mimic the rate of spring increase, and the duration and timing of warmer summertime temperatures. Similarly, water could be mixed from the epilimnion and hypolimnion in monomictic reservoirs to match natural downstream temperatures in warmer climates where reservoirs often stratify and mix once per year (e.g., tropics).

Implications for Practice

- We need to restore key components of the full range of all factors that historically maintained diversity for restoration to be successful.
- Restoring only the natural flow regime may not be sufficient to restore historic levels of diversity, especially downstream from dams with a deep release.
- Restoration of the natural thermal diversity will have a great impact on restoring macroinvertebrate diversity in many regulated rivers.
- Modern dams can release water to the downstream community from various depths within the reservoir at the appropriate time of year to mimic key aspects of the natural temperature regime.

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