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Short-term changes in channel form and macroinvertebrate communities following low-head dam removal

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Abstract. Although >70 dams have been decommissioned in Wisconsin over the past 30 y, little is known about the physical and ecological effects of dam removal on riverine ecosystems. The purpose of our study was to document changes in channel form and macroinvertebrate assemblages following the removal of a low-head, run-of-river dam from the Baraboo River, Wisconsin, in January 2000. We surveyed cross sections and collected benthic macroinvertebrate samples in 6 reaches (an upstream reference reach, reaches immediately above and below the dam that was to be removed, and sequential unimpounded and impounded reaches further downstream) in a multiple-dam system. Surveys were conducted in December 1999, before dam removal, in March 2000 immediately after dam removal, and in August 2000 following a flood. Benthic sediments were collected from selected sites in March and August to measure particle size shifts associated with the dam breach. Before dam removal, impounded reaches were characterized by relatively deep, wide channels, extensive deposits of loose sediments, and macroinvertebrate taxa characteristic of lentic or depositional habitats. Removal of the dam significantly decreased the cross-sectional area of the active channel in the former impoundment from 59 m^2 to 11 m^2, but did not alter channel form in downstream reaches. However, we found an increase in loose sediments and in the relative abundance of the sand fraction (0.5–2.0 mm) below the dam immediately after it had been removed. A flood in June increased cross-sectional area in the former impoundment by widening the channel. Sediments that had settled in the reaches below the dam in March were transported ~3.5 km downstream, where they became trapped in another impoundment. The flood had little or no detectable effect on the other 5 study reaches. Within 1 y of dam removal, macroinvertebrate assemblages in formerly impounded reaches did not significantly differ from those in either the upstream reference site or in other unimpounded reaches below the dam site. All unimpounded sites were characterized by lotic taxa such as net-spinning caddisflies and heptageniid mayflies regardless of their impoundment history. Thus, dam removal caused relatively small and transient geomorphic and ecological changes in downstream reaches, and apparently rapid channel development to an equilibrium form within the impoundment, associated with both dam removal and the subsequent June flood. These muted changes and rapid recovery likely result from the relatively large channel size and the small volume of stored sediment available for transport following dam removal.

Key words: dam removal, impoundment, sediments, transport, erosion, deposition, macroinvertebrates, river restoration, flood, Wisconsin.

There is now a well-established body of literature documenting the widespread occurrence of dams and their profound physical, chemical, and biological effects on riverine ecosystems (Baxter 1977, Petts 1984, Dynesius and Nilsson 1994, Collier et al. 1997, Graf 1999, Rosenberg et al. 2000). Although dams have provided substantial economic benefits, these benefits have come at the cost of fundamental alteration of lotic systems. Growing awareness of

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the significance of the ecological costs of dams coupled with the aging of many of these structures has prompted serious consideration of dam removal as a viable management option.

Waterways in the State of Wisconsin support nearly 4000 dams (Gebken et al. 1995). Many of these structures are low-head, run-of-river dams, that is, structures that create a hydraulic head typically <7.5 m and do not substantially alter the natural flow regime of the river. State and federal laws mandate relicensing on either a 10- or 50-y cycle, and in Wisconsin (and elsewhere in the USA), many dams are scheduled for re-evaluation within the current 5- to 10-y window. Inspections have highlighted diminished economic returns, structural weaknesses, and environmental damage; and increasingly, natural resource managers are favoring removal rather than repair and relicensing of aging structures (Born et al. 1998). More than 70 dams have been decommissioned in Wisconsin over the past 30 y, and 25 of these removals have occurred since 1995 (American Rivers et al. 1999). The relatively high rate of removal in the State has made Wisconsin a focal point and potential source of information for dam removals elsewhere, including the western USA where proposed removals of large structures are currently being debated (Task Committee on Guidelines for Retirement of Dams and Hydroelectric Facilities 1997, Born et al. 1998). Despite the relatively large number of removals and the attention that dam removal is now receiving, there have been remarkably few studies of the ecological changes resulting from this action. Indeed, there is only a single published article that has quantified physical and biological changes following dam removal (Kanehl et al. 1997). Consequently, there are significant gaps in our understanding of the rate and pattern of change in ecosystem structure and function following dam removal.

Our study documented changes in habitat and macroinvertebrate assemblages associated with the removal of a low-head dam from the Baraboo River, Wisconsin. In particular, we focused on changes in channel form and sediment characteristics following dam removal because the physical habitat largely governs aquatic community composition (Power et al. 1988), and because the movement of stored sediments has been identified as one of the greatest challenges associated with the removal of dams and river restoration (Shuman 1995, Task Committee on Guidelines for Retirement of Dams and Hydroelectric Facilities 1997). Specific objectives of our study were to examine short-term (1–2 y) changes in channel form, bed sediment composition, and aquatic macroinvertebrate assemblage composition following dam removal.

Study Site

Site description

The Baraboo River drains a 1699-km^2 basin in south-central Wisconsin and flows ~175 km from the headwaters to its confluence with the Wisconsin River. The dominant land use in the basin is mixed agriculture, representing ~65% of total land cover in the basin. Hydrology of the region is dominated by thunderstorm frontal systems resulting in a flashy hydrograph (Fig. 1). However, seasonal flooding is common in spring (March–May) because of snowmelt and rain-on-snow events.

The river channel lies in the valley between the North and South ranges of the Baraboo Hills throughout most of the basin. The valley between these ridges of Precambrian quartzite is filled with glacial sands and gravels overlying a Cambrian sandstone formation. Total altitude change along the mainstem channel is 46 m, but ~⅓ (14 m) of this gradient occurs within a 7-km reach historically known as the Baraboo Rapids where the river passes through the City of Baraboo. Here, the North and South ranges constrain the valley, and the channel has cut into the glacial deposits. High water velocities and the steep gradient made this reach an ideal site for exploitation of hydropower, and dam building began in the early to mid 1800s. Initial structures were composed of rock and timber cribs, but by 1929 three permanent (concrete) dams were in place within this 7-km reach (Fig. 2). All 3 structures were low-head (2.5–5 m), run-of-river dams that created small (3–15 ha) impoundments. The sequence of dams converted the rocky, high-velocity reach into a series of shorter rapids interrupted by impoundments with reduced velocities and silty substrates.

Mean channel width within the entire reach was 36 m. Water depth in unimpounded sections varied between 0.4 and 0.6 m, whereas reservoir depths were typically 1.0 to 1.5 m. How-

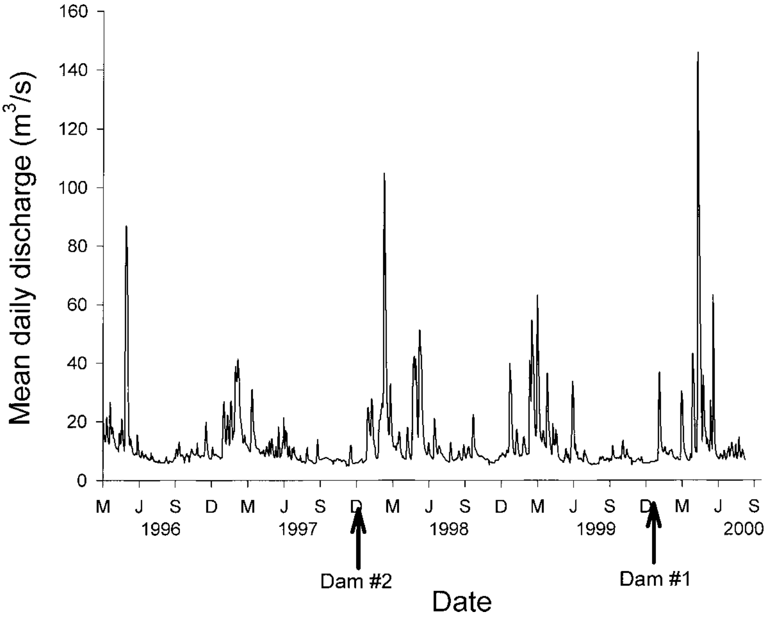

FIG. 1. Mean daily discharge between April 1996 and September 2000 in the Baraboo River, Wisconsin. Arrows indicate approximate dates of dam breaches.

ever, width of the wetted channel increased only slightly (by 15–25 m) in the impounded reaches because of the narrow floodplain.

Dam removal

The Baraboo Rapids has been the focus of restoration efforts by the Wisconsin Department of Natural Resources (WDNR); management plans called for the removal of all 3 structures to restore the high-gradient habitat. Restoration began in December 1997 with the breaching of the 2nd of the 3 consecutive dams (Dam #2, Fig. 2). The most upstream dam (Dam #1) was removed in January 2000, and changes associated with this removal were the main focus of our study. The most downstream structure (Dam #3) was removed in October 2001.

Dam #1 was originally built of rock and timber in 1885. The concrete structure in place at the start of our study was constructed in 1929 on the downstream face of the rock and timber dam, and a downstream apron was added in 1940. The dam created an impoundment of ~6.5 to 15 ha. Because of the long impoundment history, sediment characteristics, and basin land use, sediment deposition within the impoundment has been substantial. The original impoundment water depth of ~3 m was reduced to 1 to 1.5 m just before the dam was removed, and deposited sediments were dominated by silty clay and sand (RMT Associates 1999).

Initial drawdown of Dam #1 occurred on 11 January 2000 following extraction of 2980 m^3 of coal-tar-contaminated sediment. The dam was dismantled by first removing the upper 1 m of concrete from the entire length of the dam, and then removing a 6-m-wide section from its right (south) side. The newly exposed channel banks were stabilized after complete removal of the concrete structure, which included rip-rapping, grading, and seeding with a mix of perennial prairie species.

Dam #2 was a concrete dam originally built in 1858. At the time of its removal in 1997, it was a 4.3-m-high structure that created an impoundment with a surface area of 19 ha and average and maximum storage capacities of 2.3 $\times 10^5$ and 4.9 $\times 10^5$ m^3, respectively. Restoration efforts following removal included rip-rapping of ~20 m of both banks immediately upstream of the former dam site and addition of boulders to the formerly impounded channel to increase habitat heterogeneity.

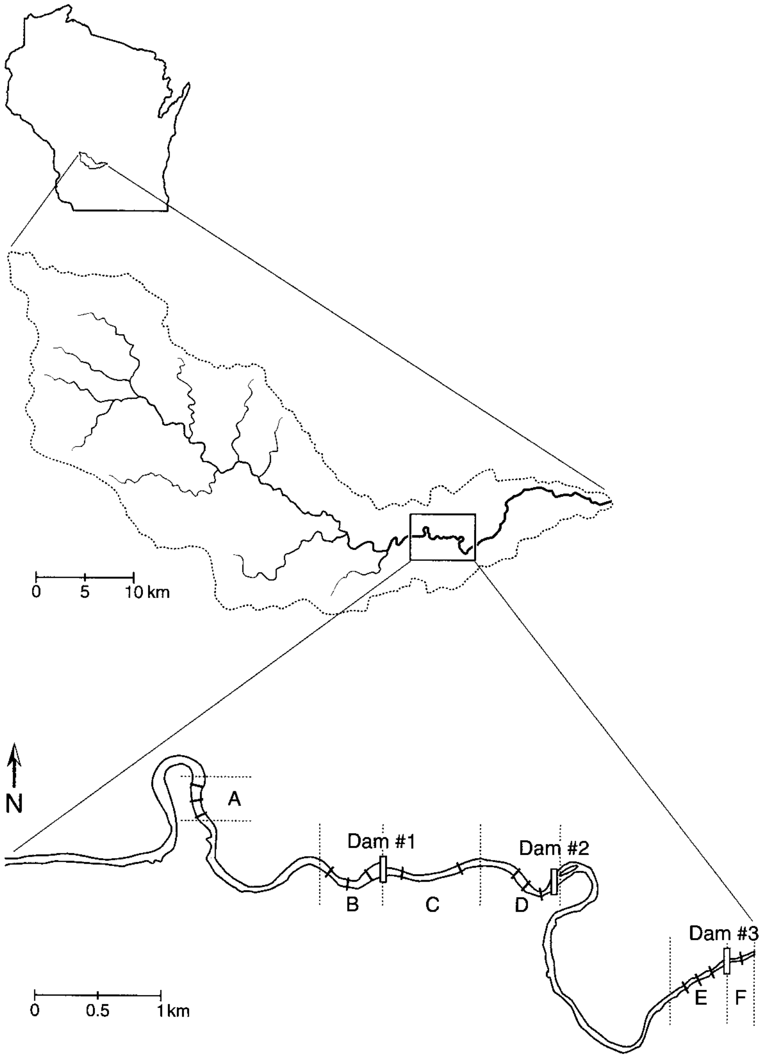

FIG. 2. The Baraboo River basin and the Baraboo Rapids study area, Wisconsin, designating locations of dams, study reaches, and transects used to monitor channel cross sections from 1999 to 2000. Dotted lines indicate reach boundaries.

Methods

The Baraboo Rapids study area was divided into 6 reaches based on impoundment history and proximity to a dam (Fig. 2, Table 1). Reaches from upstream to downstream were: never impounded (A), in the impoundment created by Dam #1 (B), the lotic zone downstream of Dam #1 (C), in the former impoundment area of Dam #2 (D), in the impoundment of Dam #3 (E), and immediately downstream of Dam #3 (F). Three permanent cross-sections separated by distances equal to twice the mean channel width of each reach were established in reaches A, B, D, and E for documenting spatial and temporal changes in channel form associated with removal of Dam #1. Transects in Reach B were situated just upstream of the area affected by bank-grading activities following dam removal. Two transects were established in Reach C and 1 transect in Reach F for assessing channel change immediately below the dams over the course of the study.

TABLE 1. Reach and transect attributes and location of dams within the Baraboo Rapids study area, Baraboo River, Wisconsin.

Reach	Hydrologic attributes	Habitat attributes	Transect distances from Dam #1 (m)
A	Free-flowing (never impounded)	Boulder–cobble–sand riffle–run	−1750, −1690, −1630
B	Impounded until Jan. 2000	Silt and poorly sorted sand in impoundment	−384, −256, −128
	Dam #1		0
C	Free-flowing (never impounded)	Boulder–cobble–sand riffle–run	128, 378
D	Free-flowing since Dec. 1997	Silt, sand, cobble run	918, 1004, 1090
	Dam #2		1176
E	Impounded	Silt, sand in impoundment	3586, 3662, 3738
	Dam #3		3814
F	Free-flowing (never impounded)	Silt–sand run	3900

Channel cross-sectional morphology

Cross-sectional profiles were surveyed in December 1999 (pre-removal), then again in March and August 2000 after dam removal. Permanent benchmarks were established for each transect. In December, the line between benchmarks was used only as a guide, and channel depth was determined from the water surface. In the March and August surveys, channel depth was measured from both the water surface (for the wetted portion of the cross-section) and from a level survey line established between benchmarks on each bank. This 2nd set of depth measurements was used to characterize the channel cross-section beyond the edge of the water and to normalize estimates of cross-sectional area among dates (see below). In all months, depth measurements were made at 1-m intervals. Loose sediment depth (hereafter referred to as sediment depth) was determined by pushing a rod into the sediments to the point of resistance. This measurement was not intended as a means of determining total sediment depth, but instead was used for quantifying fine sediment changes associated with dam removal. The method is useful for assessing recent fluvial deposition, particularly in the case of fine deposits overlying coarser material deposits (e.g., Lisle and Hilton 1992). Discharge was measured at a US Geological Survey gauging station 3 km below the study reach.

Cross-sectional area of the channel was calculated for each 1-m interval across a transect using field measurements of depth, and summed across the entire channel width. Cross-sectional areas were determined only for the wetted channel in the December survey. Because discharge varied among survey dates, the data were normalized to reflect the cross-sectional area of the wetted channel for the mean survey-day discharge of 8.3 m^3/s. The uncorrected (field-measured) cross-sectional area was multiplied by the ratio between mean survey-day discharge and discharge on the specific field day to normalize the cross-sectional area. Location of the normalized water surface was determined for each individual cross-section by fitting this area difference to each cross-section. It should be noted that this approach does not document the bankfull channel form, and it assumes that there is no change in water velocity over the range of observed discharges. Undoubtedly, this assumption introduces error into estimates of normalized cross-sectional area and form. However, the variation in discharge among dates was relatively small (7.3–9.2 m^3/s), channel areas were relatively large, and observed changes caused by dam removal were substantial, so it is likely that the error introduced by this assumption is relatively small.

Differences in cross-sectional area and sediment depth among dates for reaches A, B, D, and E were evaluated with a repeated-measures analysis of variance (RM-ANOVA) on natural-log-transformed data using SYSTAT (version 9.0, SPSS Inc., Chicago, Illinois) after confirming that the transformation satisfied assumptions of the ANOVA. Significant differences among dates for any one site, and differences between sites during the initial December survey, were identified using Tukey's multiple comparison method.

Bed material composition

Triplicate bulk samples of bed material were collected from the upper 5 to 10 cm of each transect in Reaches B, C, and D in March and August 2000 for assessing changes in substrate composition following dam removal. Assuming a median grain size of 16 mm (likely to be a conservative estimate for our study area) and a moderately well-sorted grain-size distribution in the bed sediment, the amount of material needed to describe changes in the general bed sediment composition should be at least 114 g (following the methods of Ferguson and Paola 1997). Grab samples were taken 1 to 2 m from each bank and from the center of the channel. Individual sample sizes ranged from 50 g to 100 g (dry mass), so sediments were composited for each transect, producing a final sample mass >114 g. Sediment size distribution (as % of total sample mass) for silt and clay (<0.05 mm), sand (0.05–2.0 mm), and gravel (>2.0 mm) fractions were determined by drying and sieving the composited samples (Knighton 1998).

Macroinvertebrates

Macroinvertebrate samples were collected annually or biannually between 1996 and 2000 in reaches A, B, C, and E, and in the riffle section below Reach D between 1997 and 2000 to assess broad-scale changes in benthic assemblage structure over the course of dam removal. This longer sampling time-frame allowed us to consider impacts of the removal of both dams. Invertebrates were collected by timed sampling (4 min) using a 30 cm D-frame net except for the initial sampling within Reach D in 1997. A core sampler (6.1 cm diameter) was used for the initial Reach D collection, but there were no obvious differences in sampling efficacy between the 2 methods in terms of taxonomic composition, and so the D-net was subsequently used at all sites on all dates. In most years, triplicate samples were collected in late spring (April–May) within lotic reaches and 5 to 9 replicates were taken in a stratified fashion along the length of impounded reaches. In addition, single samples were collected on an opportunistic basis from lotic sites in November 1999 and 2000 to supplement the extent and frequency of the basic sampling effort. Samples were preserved in ethanol for later sorting and identification. Insects were identified to genus, but taxonomic resolution was usually restricted to order for noninsect invertebrates.

Spatial and temporal differences in macroinvertebrate assemblages were evaluated using the Hilsenhoff Biotic Index (HBI, Hilsenhoff 1987) and multivariate statistical techniques. The HBI is an indicator of habitat quality based on differences in invertebrate tolerances to organic pollution, and uses genus-level macroinvertebrate abundance data. Multivariate methods of classification and ordination included a hierarchical classification using the CLUSTER routine in the PRIMER package (Clarke and Warwick 1994), which yielded a dendrogram illustrating relationships among samples based on their Bray–Curtis similarities. This classification approach is especially useful when groups are expected to occur (such as before and after dam removal). However, if complex gradients are possible (e.g., seasonal or longitudinal trends), ordination plots are useful supplements to classification dendrograms because trends may be evident along >1 axes of similarity (Gauch 1982). Therefore, we also ordinated the data using nonmetric multidimensional scaling (NMDS) computed by the MDS subroutine in PRIMER. Nonmetric multidimensional scaling maps the samples in ordination space such that the rank order of the distances among samples on the plot matches their Bray–Curtis similarities, and samples that share similar assemblage composition will group together. The degree to which the plot represents true relationships in a given dimension is represented by a stress value (<0.20 is considered acceptable; Clarke and Warwick 1994).

We used a multivariate ANOVA that performs a nonparametric test of between- versus within-group differences on the similarity matrix to test hypotheses of differences in macroinvertebrate assemblages between unimpounded versus impounded sites and effects of impoundment history (Clarke 1993). This test in the ANOSIM routine of PRIMER generates a *global R* statistic contrasting "within" and "among" distances, and compares the *R* statistic with *R* values calculated from 10,000 random permutations of the original data to establish a significance level for the hypothesized groupings to occur by chance.

Multivariate analyses were run on an abridged matrix of 27 composite samples of invertebrate abundances averaged across replicates. Replicates for each site–date combination were averaged because of differences in the number of replicates collected, and to emphasize individual reaches (rather than individual samples) as replicates for statistical analyses. Classification and ordination using all replicates verified that results derived from the larger matrix of all 86 samples were not qualitatively different from results of analyses based on means.

Results

Cross-sectional morphology

Channel form varied significantly ($F = 173.66$, $p < 0.001$) among study reaches prior to dam removal (Fig. 3, top). Channels in impounded Reaches B and E were ~1 m deeper and cross-sectional areas were 35 to 45 m^2 greater than in unimpounded reaches. Cross-sectional area of the upstream reference Reach A was not significantly different from Reach D, the reach formerly impounded by Dam #2. The channel forms in Reaches A, C, D, and F appeared similar, in terms of width and depth and the relatively uneven bed surface. Sediment depth followed a similar pattern in that there were significant differences among reaches ($F = 31.90$, $p < 0.001$): unimpounded reaches had ≤5 cm of loose sediment, compared to >10 cm in both impoundments in December 1999 (Fig. 3, bottom).

As expected, removal of Dam #1 caused significant changes in channel form in the reach just above the dam, and in several downstream sites (Figs 3, 4). Differences among reaches across survey dates (i.e., date × reach effects) were significant for both cross-sectional area ($F = 39.10$, $p < 0.001$) and sediment depth ($F = 5.21$, $p < 0.01$). Mean channel cross-sectional area in Reach B decreased from 59 m^2 to 11 m^2 because of drastic reductions in channel width and comparatively modest increases in channel depth, both associated with channel incision into the reservoir sediments (Fig. 4B). Breaching of the dam scoured the channel to a depth of 1 m immediately downstream (Fig. 4C), producing a slight increase in mean cross-sectional area of this section of the river. Although there were no significant changes in the cross-sectional areas within Reaches D and E, sediment depth in this section of the river increased significantly following dam removal (Fig. 3).

The Baraboo River flooded during the first week of June 2000, with instantaneous and mean daily discharges rising to 156 m^3/s and 146 m^3/s, respectively. The flood caused obvious local scouring as well as reach-scale mobilization and transport of sediments, particularly in the immediate vicinity of the dam removal site. The incised channel in Reach B maintained a consistent depth, but widened ~10 m (Fig. 4B), resulting in a significantly larger cross-sectional area after the flood (Fig. 3, top). In Reach C, changes in cross-sectional area were dominated by filling-in of the scour hole that had been created by the dam breach on the right side of the channel. Scouring of the thalweg (i.e., along the left bank; Fig. 4C) decreased sediment depth for the reach (Fig. 3, bottom). Substantial amounts of sediment were deposited in the impoundment at Reach E and below Dam #3 in Reach F, causing channel area to decrease and sediment depth to increase in this section of the river (Figs 3 top, bottom; 4E, F). Greatest sediment deposition occurred along channel banks. In Reach F below Dam #3, these deposits reduced the channel depth by ~0.5 m on the left bank (Fig. 4F).

Bed material composition

Dam removal exposed extensive deposits of accumulated sediment throughout the former impoundment. Bank erosion following drawdown revealed a sediment structure typified by 2 relatively distinct layers: a band of silty mud of variable thickness on top of sand of unknown depth. Post-removal observations suggest that fine sediments (silts) were easily mobilized by channel flow, thus exposing the underlying sand layer to downstream transport. The sand fraction increased noticeably below the dam site (Fig. 5, top), and sand from the impoundment was deposited on channel margin bars, at the downstream end of existing in-channel bars, and along some overbank areas in Reach C. Deposition of fines occurred in limited areas of Reach D, such as at the 928 m collection point. However, most material deposited in the kilometer below the dam was dominated by the sand fraction (Fig. 5, top). The June flood sub-

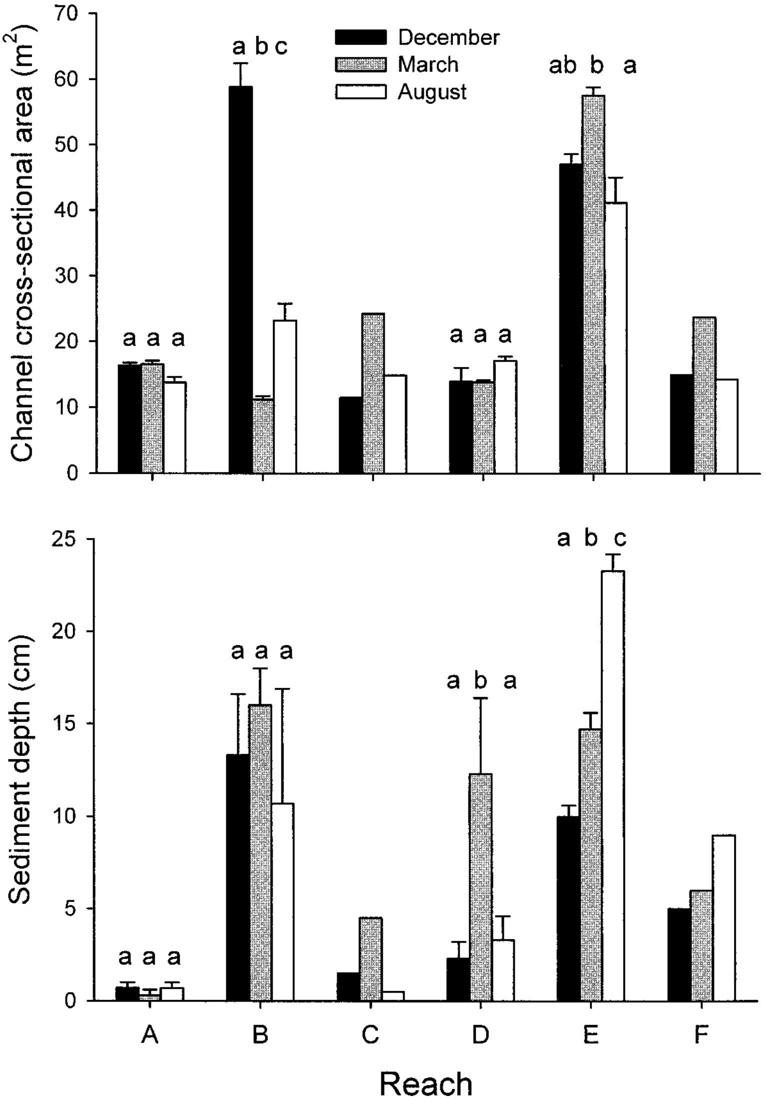

FIG. 3. Mean cross-sectional area (top panel) and sediment depth (bottom panel) in the 6 study reaches of the Baraboo River. Error bars represent +1 SE. Small letters above bars show results of multiple comparison tests within individual reaches; bars with different letters indicate significant ($p < 0.05$) differences among months within the reach. Reaches C and F were not included in statistical analyses because of the limited number of transects in these reaches.

stantially altered sediment composition above and below the former dam. Fine sediments were more abundant and sand was less abundant above the dam site in August than in March, whereas flooding shifted sediment composition from sand to gravel dominance in Reaches C and D (Fig. 5, bottom).

Macroinvertebrates

A total of 107 taxa was collected from the 6 reaches between 1996 and 2000. The number of taxa occurring in lotic sites (91) was almost twice that of impounded sites (48), and there was no overlap among the 10 most abundant

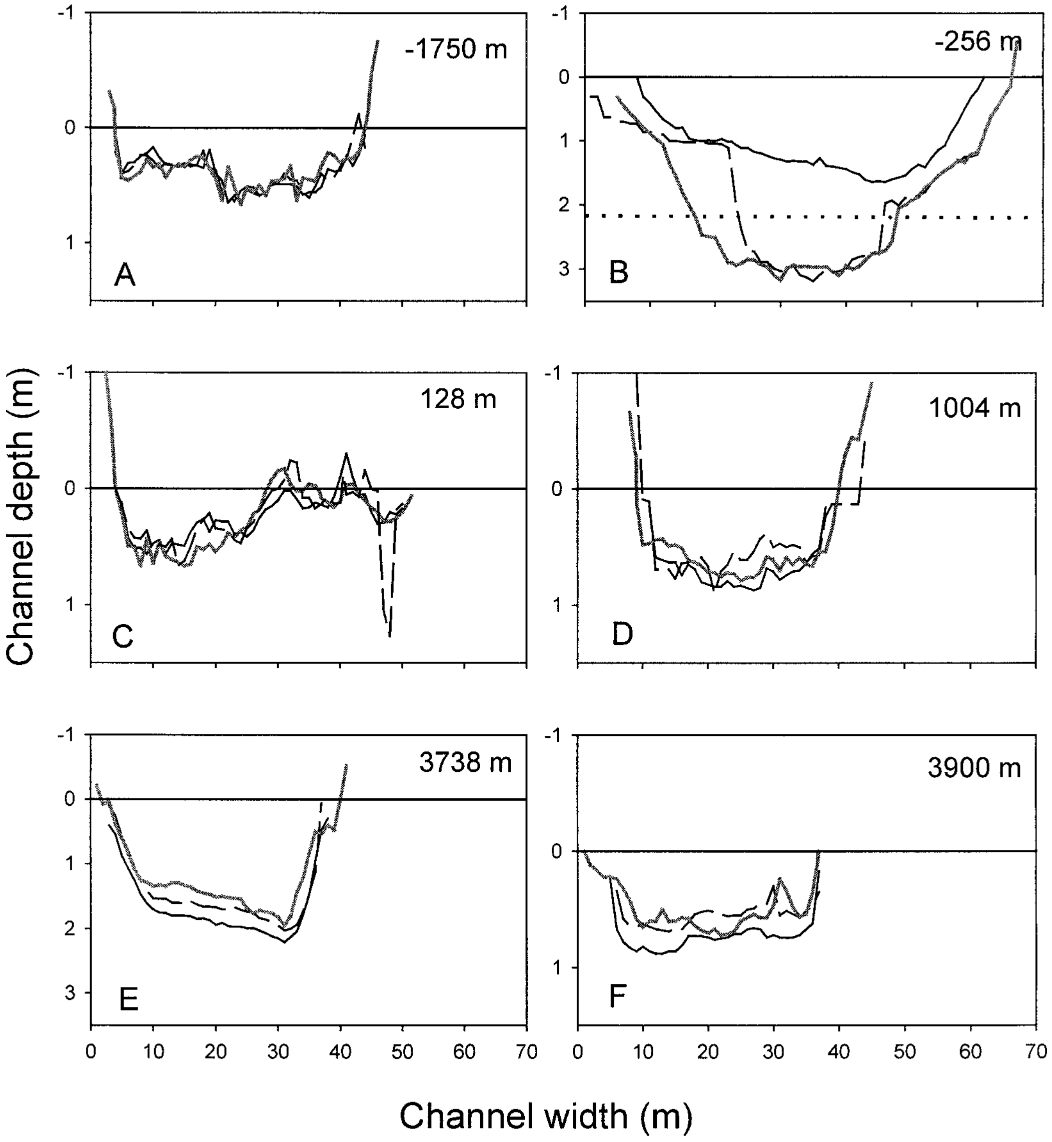

FIG. 4. Representative cross-sections from study reaches above (A, B) and below (C–F) Dam #1 prior to removal (December; solid line), immediately following removal (March; dashed line), and after a flood (August; gray line). Channel depth in all examples except the −256 m cross-section represents distance from the water surface (= 0 m), standardized to a mean study period discharge of 8.3 m^3/s. For the Reach B transect, cross-sections are relative to the water surface in December prior to dam removal; approximate water surface in March and August is indicated by the dotted line.

taxa in each habitat type. Tubificid worms and the chironomids *Chironomus* and *Polypedilum* accounted for 59% of all individuals collected in impounded reaches. Several other chironomid genera and burrowing mayflies were also prevalent at these sites. Free-flowing reaches (which included the upstream reference site, reaches below dams, and reaches above dams following removal) were dominated by two net-spinning caddisflies (*Cheumatopsyche* and *Ceratopsyche*), naidid worms, the chironomid *Orthocladius,* and a heptageniid mayfly (*Stenonema*), representing 56% of all individuals in these reaches.

HBI scores were relatively similar among all

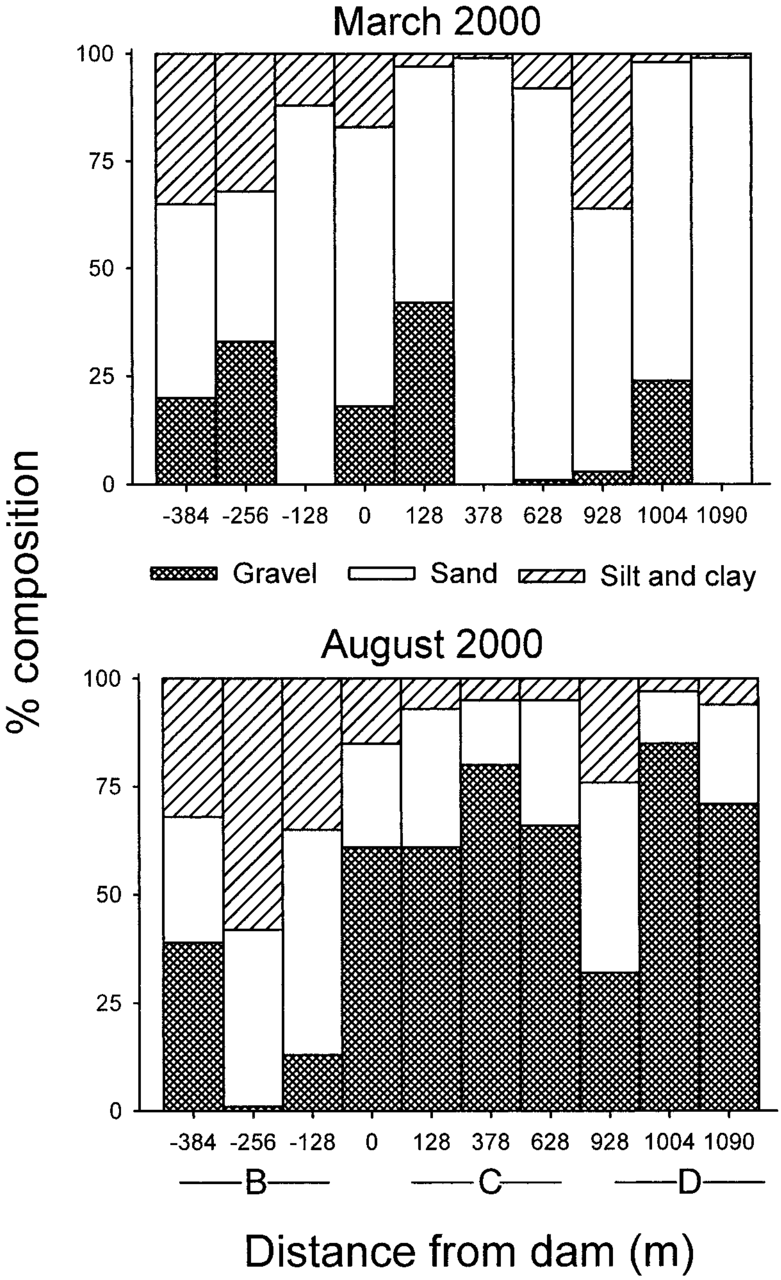

FIG. 5. Relative composition (as % of total sample mass) of sediment size fractions along a longitudinal transect from 384 m above to 1090 m below the Dam #1 removal site (0 m), March and August 2000. Reaches for individual sampling points are indicated on the x-axis. Fine sediments <0.05 mm; sand = 0.05–2.0 mm; gravel >2.0 mm.

site–date combinations, except for samples collected in the impoundments in Reaches B and D, and varied between 5 and 6 (Fig. 6), representing ''good'' to ''fair'' conditions (Hilsenhoff 1987). Average HBI scores for 2 of the 3 impoundments (Reach D in May 1997 and Reach B in 1998) were >7, characteristic of poor water-quality conditions (Hilsenhoff 1987). However, the HBI for the 3rd set of samples from an impounded reach (Reach E in 2000) fell within the range typical of lotic sites (Fig. 6).

Both the Bray–Curtis classification (Fig. 7) and NMDS ordination (not shown) confirmed the strong divergence in composition between the lentic and lotic assemblages. Stress level for the NMDS ordination equaled 0.05, and ANOSIM of differences between impounded and unimpounded assemblages was significant (*global* $R = 1.00$, $p < 0.05$). The 1st division of the hierarchical dendrogram separated all lotic samples from all lentic samples (Fig. 7). Among the lotic sites, there were no apparent differences in macroinvertebrate assemblage structure with respect to location or impoundment history. Instead, the dendrogram results indicated that assemblage differences among lotic sites were associated with seasonality rather than impoundment history (Fig. 7). All lotic samples fell in a tight cluster in the ordination plot and ANOSIM indicated no significant differences (*global* $R = -0.08$, $p = 0.71$) among lotic sites that had never been impounded (Reaches A, C, and below Dam #2) and newly formed lotic sites created by dam removal (Reach B in 2000 and Reach D after 1998).

Discussion

Effects of low-head dams

Low-head dams in the Baraboo Rapids study area created distinct physical and ecological conditions relative to free-flowing lotic reaches despite the constrained channel and small sizes of the dams. As expected, impounded reaches were broader and deeper, contained extensive deposits of loose sediment, and had reduced current velocities. Yet, although macroinvertebrate HBI scores generally indicated poor water quality in the impoundments, low-head dams did not alter chemical attributes of the water such as temperature and dissolved oxygen in the lower Baraboo River (DWM and EHS, unpublished data). The dams were run-of-river structures with relatively small impoundment areas and, therefore, they did not have any noticeable effect on the overall flow regime in this section of the river. Nonetheless, changes in current velocity and bed sediment composition were sufficient to cause marked divergence in macroinvertebrate assemblages between impounded and free-flowing reaches. Characteristically lentic taxa such as tubificid worms, the hemoglobin-rich chironomid *Chironomus*, and burrowing mayflies (*Hexagenia*) prevailed in impounded reaches, whereas net-spinning caddisflies and heptageniid mayflies typified lotic sections of the river. The HBI scores were less sensitive than the nonparametric analyses in revealing this divergence, given that samples from Reach E in 2000 had scores similar to lotic sites throughout the study. Better HBI scores for Reach E were apparently the result of reduced numbers of individuals and the presence of a limited number of typically lotic taxa (e.g., the net-spinning caddisfly *Hydropsyche*).

Although the divergence in assemblage structure between impounded and unimpounded river reaches does not seem surprising, the ecological consequences of low-head dams are poorly understood (Benstead et al. 1999). These structures act as barriers to some invertebrates and fishes, but do not affect others. Similarly, the use of both impounded and unimpounded habitats by the same taxon varies among taxa (cf. Watters 1996, Cortes et al. 1998, Concepcion and Nelson 1999); thus, reservoirs represent inhospitable habitats for some, but not all, lotic species. However, the extent of alterations observed in this study indicates that even relatively small dams can cause profound changes in upstream benthic invertebrate populations.

Effects of dam removal

Removal of Dam #1 resulted in rapid and pronounced changes in channel morphology above the dam, and in bed sediment composition below the dam. The sudden increase in channel slope and release of impounded water associated with breaching caused downcutting into the reservoir sediments and produced a deeper, narrower channel in the former impoundment. Visual examination of exposed reservoir sediments following drawdown indicated that greater deposition of fine particles in the

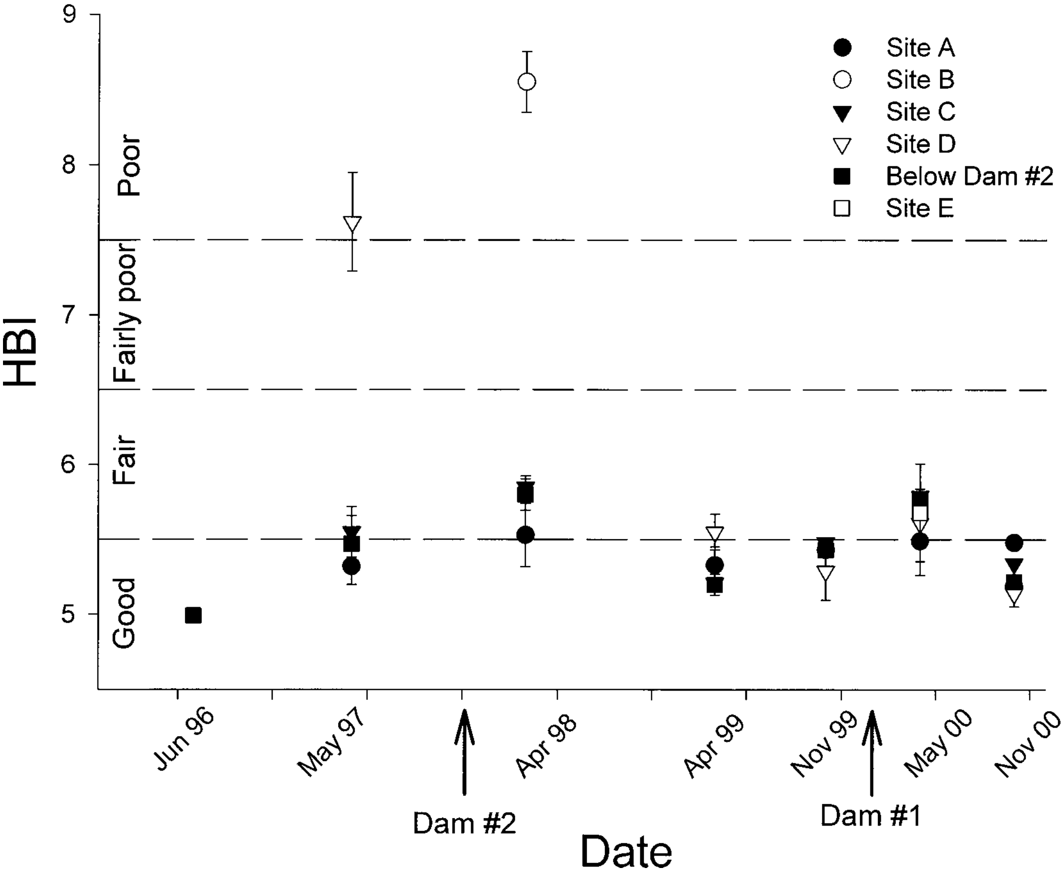

FIG. 6. Hilsenhoff biotic index (HBI) scores for macroinvertebrate assemblages between 1996 and 2000. Values are means (±1 SE). Dashed lines indicate habitat quality categories sensu Hilsenhoff (1987). Arrows indicate the approximate dates of removal for Dam #2 (January 1998) and Dam #1 (January 2000).

impoundment occurred with increasing lateral distance away from the thalweg, and that the layer of silty material was relatively thin (~20 cm) in the center of the channel area. Thus, downcutting in the reservoir area following removal is likely to have mobilized a relatively small amount of fine sediments and large amounts of sand.

Although substantial scour occurred immediately below the dam, deposition of sediments from within and just below the reservoir was apparent at distances of <500 m below the dam site. Sediment deposition did not significantly alter channel form in Reach D, but a distinct layer of fine and sandy sediments was present throughout much of this reach. Sand transported from the reservoir probably did not affect downstream channel form because mean particle size was smaller than the in situ bed sediments of this reach and, therefore, much of the deposited material would have filled interstitial voids instead of changing the channel form (Leopold 1992). However, filling of voids between larger particles has clear implications for interstitial flow through the stream bed and the potential influence of hyporheic processes on the river, such as have been observed in streams receiving high inputs of silt (Schälchi 1992). Despite this rapid change in benthic sediment characteristics, there were no obvious changes in macroinvertebrate assemblages in Reaches C or D in May 2000, either in terms of HBI scores or ordination and classification results.

Flooding in June 2000 significantly increased cross-sectional area within the former impoundment via channel widening. Channel depth did

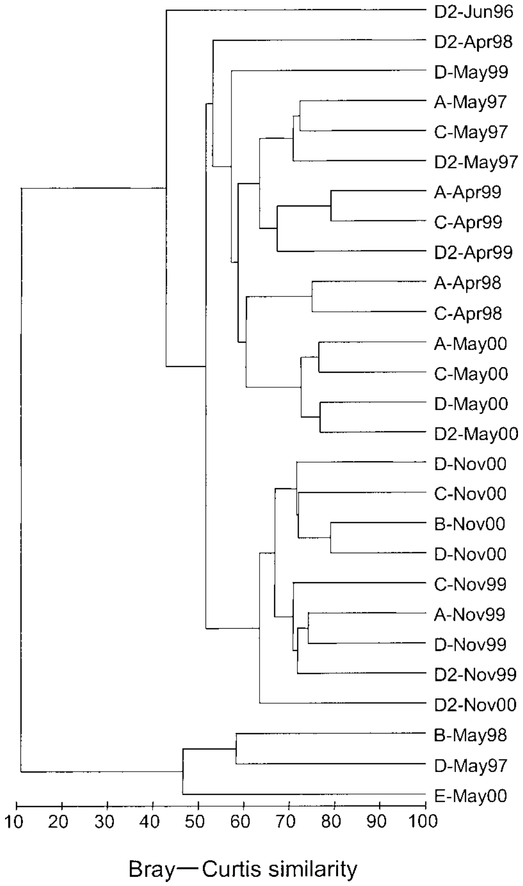

FIG. 7. Dendrogram of macroinvertebrate assemblage similarity (based on average, log-transformed data) among samples collected from the impounded and unimpounded reaches of the Baraboo River between May 1996 and November 2000. The 1st letter of the sample code denotes the reach location; Reach D2 is the reach below Dam #2.

not increase, presumably because the channel slope had reached an equilibrium. In the absence of the June flood, the relatively narrow channel with steep banks created by the breaching alone (i.e., the channel form in March) would likely have persisted once vegetation became established on the banks. Indeed, persistence of incised channel forms for >30 y following dam removal has been observed elsewhere in Wisconsin (Lenhart 2000). However, because the June flood occurred before physical stabilization of banks (consolidation of cohesive bank material and enhanced stability as a result of vegetation), it caused substantial changes throughout the reach. Similar flood-driven alterations were notably absent in all other reaches, indicating that sensitivity to flooding was amplified in Reach B relative to the rest of the river. We have seen no obvious change in the channel form since the June flooding, likely because of the absence of further flooding and the development of increased physical stability of bank sediments. This period in which floods can have disproportionately large effects on the channel can be considered a 'window of sensitivity' (Doyle et al. 2002). Long-term channel morphology can be a function of both the dam removal itself and the sequence of hydrologic events that occur immediately following removal.

Sandy sediments deposited below the reservoir following dam breaching in January 2000 were transported out of Reaches C and D following the June flood, exposing gravel that closely resembled the bed prior to removal of the dam. Even the most striking change in channel form (the scour hole created by the initial breach) was eliminated by the June flood. Sand transported out of these reaches accumulated in the downstream impoundment (Reach E), significantly reducing the volume of the reservoir. We suggest that had Dam #3 not been present, sediments from the Dam #1 impoundment would have been distributed in a thin layer over several kilometers, and cross-sectional form would not have been affected for much of the river below the dam.

Minimizing the downstream impacts of a relatively discrete bolus of accumulated sediment may represent the single most important challenge to dam removal (Shuman 1995). Models describing transport dynamics specific to dam removal do not yet exist, but the disposition of reservoir sediments can be considered in the context of sediment wave dynamics. Three conceptual models for transport of discrete sediment waves have been suggested (reviewed in Lisle et al. 1997). In the 1st model, the sediment wave can be translated downstream as a relatively distinct packet that maintains its approximate shape and volume. In the 2nd, the wave can diffuse longitudinally over time. In the 3rd, sediments show little or no longitudinal movement and under such conditions the wave can become a permanent feature of the channel. We suggest that the diffusion model (2nd model above) is likely to hold for the Baraboo River because of 3 features: 1) the ratio of channel size to the amount of sediment available for transport, 2) the decrease in slope below the Baraboo Rapids section of the river (i.e., decreasing stream power), and 3) the absence of a discrete pool–riffle formation in the channel that seems to foster wave-like translation (Wohl and Cenderelli 2000). That is, large channel size/sediment volume ratios may favor diffusional movement of the sediment bolus, whereas progressively smaller ratios may be associated with wave-like translation or no transport. However, it should be emphasized that the 1st-order mechanisms governing sediment wave transport are very poorly understood (Lisle et al. 1997) and remain a critical area of research for understanding the geomorphic and ecological effects of dam removal.

The translation and diffusion models imply differing degrees of change to benthic communities, and effects of sediment transport that differ in duration. The translating wave model describes a spatially and temporally discrete disturbance to stream fauna, with pronounced but short-term (the period between 2 floods) effects. Repeated scour and deposition can be expected to extirpate benthic communities within individual pools as the sediment wave moves downstream. In contrast, diffusion of sediments should influence a series of reaches over a relatively long stretch of channel but cause less pronounced changes. Depending on sediment particle size and total sediment volume, smothering of benthic invertebrates and clogging of interstitial spaces are possible, although no changes in invertebrate assemblages were detected in this study. Nonetheless, these 3 modes of sediment transport suggest very different effects of dam removal on downstream communities.

Changes in macroinvertebrate assemblages over the course of 2 dam removals were rapid in reaches upstream of the dams, and limited in reaches immediately below the dams. Lentic assemblages in the 2 upstream impoundments were replaced by more lotic assemblages within a year of removal, indicating rapid colonization and establishment of lotic fauna in these newly created habitats. Possible downstream effects of dam removal associated with deposition of reservoir-derived sediments were not apparent in terms of coarse-resolution HBI scores or more taxonomically detailed multivariate analyses, suggesting either little change, or swift recovery from the effects of removal. Fish assemblages also rapidly changed to a more typically riverine structure in former impoundments following the removal of the Woolen Mills dam in the Milwaukee River, Wisconsin (Kanehl et al. 1997), as well as in the lower Baraboo River. However, downstream fish assemblages have experienced decreases in abundance and species number 1 y following the first dam removal in the Baraboo River (DWM, unpublished data).

In conclusion, small low-head dams had significant effects on the physical and ecological conditions in the Baraboo River prior to their removal. Dam removal in the lower Baraboo River produced a substantial improvement in habitat quality, with only minor and short-lived deleterious effects in terms of sediment exposure upstream and deposition downstream of the dam. The relatively moderate, short-lived effects of dam removal observed in our study do not, however, suggest that dam removal will *always* result in low magnitude and/or transient alterations to a river. Sediment accumulation is large in reservoirs that form over extensive floodplains or in deep canyons, so the potential for substantial physical and biological change following removal should be expected. For example, sediment transport models have indicated that release of the large sediment deposits stored behind the Elwha Dam in Washington are likely to cause bed aggradation and increase the frequency of overbank flooding (Stoker and Harbor 1991), eliminate resident fish populations, and disrupt riparian plant communities for decades to centuries (National Park Service 1996). Given that dam removal is becoming an increasingly common management option (Born et al. 1998), the key will be to determine the impacts of sediment transport and channel formation over a range of physical settings, and to understand methods of dam removal that may minimize these impacts.

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