J. N. Am. Benthol. Soc., 2005, 24(1):192–207

Effects of removal of a small dam on downstream macroinvertebrate and algal assemblages in a Pennsylvania stream

JAMES R. THOMSON[1], DAVID D. HART[2], DONALD F. CHARLES[3],
TIMOTHY L. NIGHTENGALE[4], AND DIANE M. WINTER[5]

Patrick Center for Environmental Research, The Academy of Natural Sciences,
1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103 USA

Abstract. Dam removal is often proposed as way to restore ecological integrity to rivers and streams, but ecological responses to dam removals are poorly understood, especially for downstream benthic communities. We examined the responses of benthic macroinvertebrate and algal assemblages in downstream reaches to the removal of a small, run-of-river dam on Manatawny Creek, Pennsylvania. Benthic macroinvertebrates, algae, and habitat characteristics were monitored upstream and downstream of the dam for 4 mo before removal, 3 mo after partial removal (i.e., when the impoundment was largely eliminated but sediment remained trapped behind the remaining structure), and 12 mo after complete dam removal. Macroinvertebrate density, algal biomass, and diatom species richness declined significantly downstream of the dam following complete dam removal, but overall assemblage structure (as indicated by Nonmetric Multidimensional Scaling ordinations) downstream remained similar to upstream control sites throughout the study for both invertebrates and diatoms. Downstream impacts occurred only after the dam structure had been completely removed and sediments had been transported downstream from the former impoundment by high flows. Biotic impacts persisted for the duration of the study (12 mo after complete removal). Our results and other studies of dam removal suggest that downstream sedimentation following dam removal can reduce densities of macroinvertebrates and benthic algae and may reduce benthic diversity, but for small dams such impacts may be relatively minor and will usually be temporary.

Key words: dam removal, macroinvertebrates, algae, restoration, BACI.

Dam removal is a potentially important method of restoring ecological integrity to rivers and streams. Dams impede the flux of water, sediments, biota, and nutrients, and can strongly alter the structure and dynamics of upstream and downstream aquatic and riparian habitats and biota (Ward and Stanford 1979, Petts 1984, Poff et al. 1997). As awareness of the ecological impacts of dams has increased, and maintenance costs have risen, calls for dam removals have increased. In the United States, >500 dams have been removed in the past century; the rate of removal has increased rapidly over the past 2 decades, and is expected to increase further in coming years (Poff and Hart 2002, Stanley and Doyle 2003).

Understanding the ecological costs and benefits of removing dams is essential to making informed decisions about whether and how a particular dam should be removed. Presently, however, there is little empirical data on which to base predictions about ecological responses to dam removal. Less than 5% (~20) of all dam removals in the United States have been accompanied by published ecological studies. Most of these studies concentrated on fish and/or the impoundment area (Bednarek 2001, Hart et al. 2002). Although benthic assemblages in downstream habitats may be strongly influenced by dam removal, few published studies have examined macroinvertebrate responses (Stanley et al. 2002), and none have evaluated algal responses, in downstream reaches.

Most of the dams removed to date were relatively small structures (usually <5 m high), and small dams will probably continue to be removed at a greater rate than large dams (Poff and Hart 2002). Small dams are far more abundant than large dams, are often older (and therefore more likely to be unused or in need of repair), and will generally be less expensive to remove (Poff and Hart 2002). Despite their

---

[1] Present address: Australian Centre for Biodiversity: Analysis, Policy and Management, School of Biological Sciences, Monash University, Victoria 3800, Australia. E-mail: jim.thomson@sci.monash.edu.au

[2] E-mail addresses: hart@acnatsci.org

[3] charles@acnatsci.org

[4] benthics@comcast.net

[5] winter@acnatsci.org

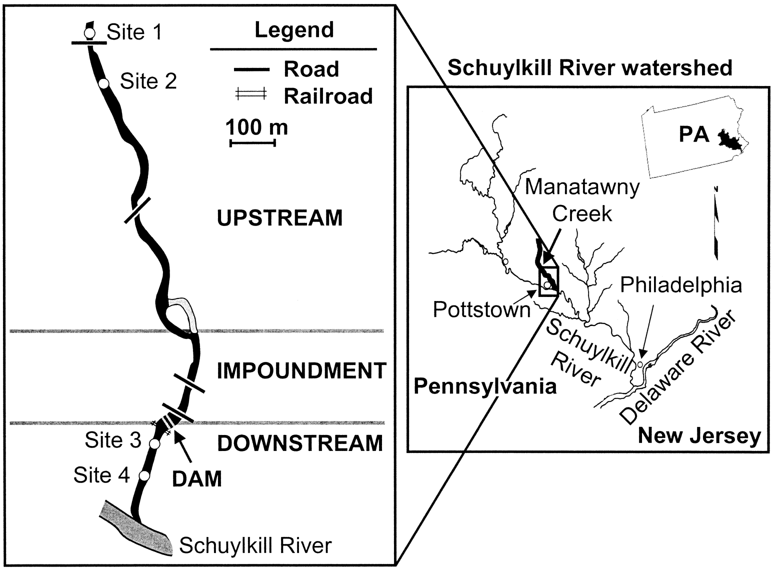

FIG. 1. Locations of Manatawny Creek, the dam, and the sampling sites.

abundance, the ecological impacts of small dams have been less studied than those of large dams (Hart et al. 2002). Limited understanding of how small dams affect flow regimes, channel form, water temperature, biogeochemical cycling, and biota (Hart et al. 2002), makes predicting the long-term ecological effects of small dam removal particularly difficult.

Removal of small dams can be expected to restore lotic habitat within the former impoundment (Bushaw-Newton et al. 2002, Stanley et al. 2002), and may improve fish passage (Stanley and Doyle 2003), but downstream benefits are less certain. For example, removing low-head, run-of-river dams that have short hydraulic residence times and limited storage volumes may have little impact on downstream water quality, thermal dynamics, or flow regimes (Hart et al. 2002). Downstream biota, particularly benthos, will not necessarily benefit from such removals.

Small dam removals may have negative effects on downstream biota. In particular, the downstream transport of sediments previously stored in impoundments has potentially serious consequences for downstream communities (Shuman 1995, Wood and Armitage 1997, Bednarek 2001, Poff and Hart 2002). Severe depletion of downstream benthos could reduce the effectiveness of dam removal as a restoration method. For example, the benefits associated with increased access by fish to upstream habitats following dam removal might be offset by corresponding reductions in food availability within downstream habitats.

We investigated the impacts of removing a small dam on downstream assemblages of macroinvertebrates and algae. Our specific aim was to determine whether there were any negative or positive downstream effects of dam removal that persisted for at least 12 mo. We also investigated the impacts of dam removal on key aspects of benthic habitat (i.e., substrate particle size and hydraulic characteristics).

Methods

Study site and sampling design

The study was conducted in the lower reaches of Manatawny Creek, a 4th-order stream in the piedmont physiographic province near Pottstown in southeastern Pennsylvania (Fig. 1). Manatawny Creek has a watershed area of 238 km^2, of which ~54% is forested, 41% is agricultural, and 3% is urban. Average annual precipitation is 1100 mm.

In the late 1700s, a run-of-river dam was built on Manatawny Creek ~500 m upstream from its confluence with the larger Schuylkill River (Chancellor 1953). The dam consisted of a timber crib surrounded by quarried boulders and was ~2 m high, 2 m thick, and 30 m across. Water was impounded for ~500 m upstream, with a hydraulic residence time at base flow of 1 to 2 h. The mean annual flow in the study area is 3.7 m^3/s, and the highest recorded flow from 1975 through 2000 was 200 m^3/s.

The dam was removed in a 2-stage process in 2000 (see Bushaw-Newton et al. 2002 for details). Following the initial excavation in August 2000, geomorphic surveys conducted in early autumn revealed that only the top meter of the dam had actually been removed. The remaining structure limited erosion of the upstream sediments and controlled the elevation of the streambed upstream from the dam (Egan 2001, Pizzuto 2002). This remaining structure was removed in late November 2000. Therefore, sampling dates were defined as pre-removal (Stage 0), partial removal (Stage 1), and post-removal (Stage 2). A benefit of the 2-stage removal process is that the partial removal period (Stage 1) provided an opportunity to examine the ecological consequences of impoundment drawdown while minimizing the effects of downstream sedimentation. On the other hand, this unplanned, 2-stage removal process complicated the sampling design. Evidence of short-term ecological responses to the complete removal in November 2000 would have required benthic sampling during winter, when abiotic and biotic conditions are markedly different from those during the warmer seasons, when most of our pre-removal sampling was conducted. Also, a large flood in December 2000 scoured the river channel and may have reduced abundances of benthic organisms, further limiting our ability to detect short-term removal impacts. For these reasons, we chose not to sample over the winter immediately following dam removal, but concentrated on the medium-term impacts of removal by sampling principally in summer and autumn, periods for which comparable pre-removal samples were available.

A modified Before-After-Control-Impact design (BACI, Green 1979) was used to study the responses of macroinvertebrate and algal assemblages in riffles downstream of the dam. Macroinvertebrates were sampled at 2 upstream control sites (Sites 1 and 2, 2.0 and 2.2 km upstream from the dam, respectively) and 2 downstream "impact" sites (Sites 3 and 4, 0.15 and 0.28 km downstream of the dam, respectively) (Fig. 1). Algae were sampled at one upstream (Site 1) and both downstream (Sites 3 and 4) sites. Samples were collected 4 times during Stage 0 for both groups, 2 (macroinvertebrates) and 3 (algae) times during Stage 1, and 5 (macroinvertebrate) and 8 (algae) times during Stage 2. Control sites were selected to be as similar as possible to impact sites. All riffles had similar dimensions (23–45 m long, ~12 m wide) with similar flow and substrate characteristics. Downstream sites had less intact riparian vegetation and received more urban runoff than upstream sites, but such differences had minimal effects on benthic assemblages (see ordination results). Importantly, the BACI study design with replicated sampling before and after dam removal tests for removal impacts by comparing the patterns of difference between control and impact sites before removal with differences after removal. Thus, initial biotic differences between control and impact sites caused by relatively static factors like riparian cover or urbanization do not prevent detection of removal impacts (Underwood 1991).

Macroinvertebrate and habitat sampling

Five Surber samples (area = 0.093 m^2, mesh = 500 μm) were collected at each site on each date. Samples were preserved in 95% ethanol. Average water velocity (directly above the bed), depth, and particle size were recorded for each Surber sample location prior to macroinvertebrate collection. Velocity was measured with a Marsh–McBirney flowmeter. Mean particle size was calculated from visual estimates of the proportion of substrate elements within the Surber area falling into each of 5 size classes (boulder >256 mm, cobble 64–256 mm, pebble 16–64 mm, gravel 2–16 mm, sand/silt <2 mm). Size classes were transformed to a phi scale ($-\log_2$ of the class midpoint) and averaged for each sample location. To ensure consistency, all substrate classification was done by a single person throughout the study. In the laboratory, macroinvertebrate samples were subsampled using a 10-cell sample splitter until at least 100 animals had been counted from each sample. Insects were identified to genus (except for family level identification of chironomid midges), and non-insects were identified to the lowest practical taxonomic level. The total number of each taxon in a sample was estimated by dividing the number in each subsample by the subsample fraction.

Algal sampling

Six randomly selected rocks (10–20 cm longest axis) from each site were sampled for periphytic algae on each date. Rock surfaces were scrubbed with a brush (or scraped with a scalpel for well-attached filamentous algae) to remove all filamentous and surface films of algae. Samples from each set of 6 rocks were composited into a single sample and stored on ice in 250 mL bottles for transport to the laboratory. After the algae were removed from the surface of each rock, the area scrubbed/scraped was estimated by creating an aluminum foil mold (Ennis and Albright 1982). Foil areas were later measured with a Placom KP-90N planimeter. In the laboratory, samples were subdivided for diatom enumeration and biomass analyses. Organic matter was removed from the diatom subsample by nitric acid digestion and samples mounted in Naphrax™ (Charles et al. 2002). Chlorophyll *a* concentrations and ash-free dry mass (AFDM) were determined using standard methods (APHA 1995).

Diatom identification and enumeration

Five hundred frustules or 1000 valves were counted for each sample using a Zeiss Axioskop at 1000× magnification. Diatoms were identified to species or variety following the nomenclature of the Phycology section at the Academy of Natural Science, Patrick Center for Environmental Research (Patrick and Reimer 1966, 1975, Krammer and Lange-Bertalot 1986–1991).

Data analyses

A combination of univariate analyses of community metrics and multivariate ordinations was used to examine macroinvertebrate and algal responses to dam removal. Factorial analysis of variance (ANOVA) models were used to examine the effects of dam removal on the following macroinvertebrate and algal metrics: total macroinvertebrate density, macroinvertebrate taxa richness, number of Ephemeroptera, Plecoptera, and Trichoptera taxa (EPT richness, Barbour et al. 1999), Hilsenhoff's Biotic Index (HBI, Hilsenhoff 1987), chlorophyll *a* biomass, diatom species richness, and diatom siltation index (% individuals from genera with mostly motile species, Bahls et al. 1992). Macroinvertebrate richness and EPT scores were standardized to the number of taxa expected in a sample of 100 individuals. Walsh's (1997) Microsoft Excel™ macro was used to generate 10 random subsamples of 100 individuals for each sample, and the average total and EPT taxa richness were calculated.

Changes in macroinvertebrate metrics and habitat variables were examined using a 4-factor ANOVA model with Location (upstream and downstream) and Stage (0, 1, and 2) as fully crossed, fixed factors, and Site (fixed) and Date (random) as nested factors. Significant Stage × Location interactions indicated possible dam removal impacts (Underwood 1991), and were followed by simple main effects tests (Stage means compared within each Location and vice versa, Quinn and Keough 2002) to determine how temporal patterns differed between upstream and downstream sites. Means for significant interaction and main effects were compared as *t*-tests using variance estimates and degrees of freedom derived from appropriate mean square estimates (Jaccard 1998).

A similar ANOVA model was used to test changes in algal metrics, but because there was only one upstream control site there was no Location term in the model. Instead, the Site × Stage term and subsequent contrasts were used to identify possible dam removal effects (Underwood 1994). Following a significant Site × Stage interaction, variance was repartitioned and the Site × Stage term tested for downstream sites only ($\mathrm{Site}_{\mathrm{down}}$ × Stage). If the $\mathrm{Site}_{\mathrm{down}}$ × Stage term was nonsignificant, the (consistent) temporal pattern at downstream sites was compared to the temporal pattern at the upstream control site by testing a $\mathrm{Site}_{\mathrm{down\ vs\ up}}$ × Stage term, and by conducting simple main effects tests on upstream and combined downstream means. Algal samples collected in spring 2001 (i.e., the first 3 post-removal samples) were not included in ANOVA because no pre-removal spring samples were collected and their inclusion would have created a very unbalanced design.

Assumptions of normality and variance homogeneity were checked with box and residual plots and appropriate diagnostic tests, and were

TABLE 1. ANOVA results for habitat variables. The denominator mean square terms used in F-tests for each term are indicated by numbers in parentheses (corresponding to superscript term numbers) after each term. No number is shown when that term was tested against the residual error. Letters in parentheses after a factor indicate that the factor is nested within Location (L) or Stage (S). p-values in bold are significant at $\alpha = 0.05$.

		Mean phi			Mean water velocity			Mean water depth		
	df	SS	F	p	SS	F	p	SS	F	p
^{1}Location (6)	1	1.113	1.251	0.296	0.000	0.000	0.999	35.415	6.864	**0.031**
^{2}Stage (5)	2	72.706	30.591	**<0.001**	3.492	2.698	0.127	160.947	1.229	0.343
^{3}Location × Stage (6)	2	8.744	4.915	**0.041**	0.022	1.059	0.391	5.138	0.498	0.625
^{4}Site(L) (8)	2	5.046	8.419	**0.003**	0.003	0.139	0.871	110.975	14.629	**<0.001**
^{5}Date(Stage)	8	9.507	1.188	**<0.001**	5.177	5.325	**<0.001**	524.024	24.567	**<0.001**
^{6}Location × Date(S)	8	7.117	0.890	**0.006**	0.081	0.084	0.999	41.279	1.935	0.057
^{7}Stage × Site(L) (8)	4	3.437	2.867	0.058	0.024	0.547	0.704	13.016	0.858	0.510
^{8}Site(L) × Date(S)	16	4.795	0.300	0.515	0.178	0.091	0.999	60.688	1.423	0.136
^{9}Residual	176	55.278			21.386			469.272		

always met by either raw or log-transformed data.

Changes in macroinvertebrate and diatom assemblage structure (i.e., the species present and their relative abundances) following dam removal were examined with Nonmetric Multidimensional Scaling (NMDS) ordinations (Clarke and Warwick 1994) using Bray–Curtis similarity matrices derived from square-root-transformed data. For macroinvertebrate data, separate ordinations were performed using individual and pooled (by site and date) Surber samples. Patterns from both ordinations were similar, but pooled samples resulted in a lower stress value (0.18 vs 0.23 for 2 dimensions) and only this ordination is presented.

Correlations between NMDS axis scores and square-root-transformed counts of each taxon were examined to determine which taxa contributed most to the distribution of samples in ordination space. In addition, the SIMPER routine in the Primer software package (Clarke and Warwick 1994) was used to identify the taxa that contributed most strongly to differences among locations (macroinvertebrates) or sites (diatoms) within each dam removal stage.

Results

Substrate and hydraulic characteristics

Mean particle size was significantly smaller (higher phi value) at all sites during stage 2 (mean phi ± SE: upstream = −4.3 ± 0.3, downstream = −3.6 ± 0.2) than during stages 0 (mean phi ± SE: upstream = −5.1 ± 0.2, downstream = −5.2 ± 0.2) or 1 (mean phi ± SE: upstream = −4.9 ± 0.3, downstream = −5.0 ± 0.3), but the average decrease (increase in phi) was significantly greater at downstream than at upstream sites (Table 1, Fig. 2). The changes in mean particle size mainly reflected increases in the % of sand from 1% to 15% at downstream sites, and from 3 to 10% at upstream sites, following complete dam removal.

Hydraulic characteristics within sampled areas did not vary among stages (Table 1). Upstream riffles (mean depth ± SE = 8.4 ± 0.2 cm) were slightly deeper than downstream riffles (mean ± SE = 7.6 ± 0.3 cm) throughout the study, but mean velocities were similar at all sites (mean ± SE = 0.43 ± 0.01 m/s for both upstream and downstream sites).

Macroinvertebrates

Macroinvertebrate densities downstream of the dam were significantly lower (by ~60%) in Stage 2 than during stages 0 and 1, with no significant difference between stages 0 and 1 (Tables 2, 3, Fig. 3A). In contrast, densities at upstream sites did not vary significantly among any stages. There was no evidence that dam removal affected the other macroinvertebrate metrics: Location × Stage interactions were not significant for total richness, EPT richness, and HBI (Tables 2, 3). Downstream sites had significantly lower overall richness and lower EPT richness than upstream sites throughout the study (Tables 2, 3, Fig. 3B, C). HBI scores for all sites generally fell within the "Good" range (<5.5),

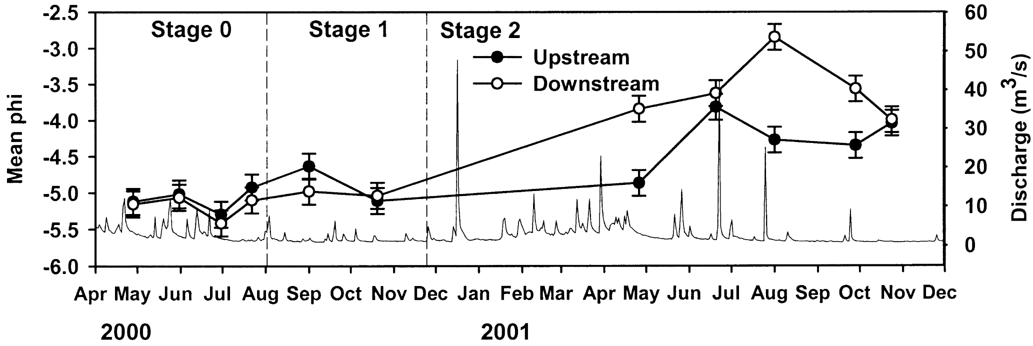

FIG. 2. Changes in mean particle size (mean phi) upstream and downstream of the dam over the study period. Points are location means (±1 SE, n = 2 sites per location). Initial and final removal events are indicated by vertical dashed lines (Stage 0 = pre-removal, Stage 1 = partial removal, Stage 2 = post-removal). Hydrograph shows timing of flood events. Hydrograph data were obtained from US Geological Survey gauging station number 01471980 (lat 40°16′22″, long 75°40′49″) located ~4.5 km upstream from the dam.

but were significantly higher (higher pollution tolerance) at downstream sites than at upstream sites throughout the study (Tables 2, 3, Fig. 3D).

The macroinvertebrate NMDS ordination (Fig. 4) indicated a seasonal trend along Axis 1, with all sites moving from right to left from spring through autumn in both years. There was some separation of upstream and downstream sites along axis 1, with downstream sites having higher scores than upstream sites on most dates, but this pattern was not affected by dam removal. The seasonal pattern reflects summer (e.g., Hydropsychidae, *Baetis*, *Acentrella*, *Serratella*, Simuliidae) or autumn (e.g., *Optioservus*, *Cheumatopsyche*, Planariidae) density peaks of common taxa. The consistent separation of upstream and downstream sites along the first axis mainly reflects higher chironomid and lower *Optioservus* densities at downstream sites. Axis 2 was most strongly (negatively) correlated with chironomid densities, and there was a general trend for all sites to move up this axis with time, reflecting lower densities of chironomids and other common taxa (*Prosimulium*, Hydrachnida, *Serratella*, Oligochaeta, *Tricorythodes*, *Stenonema*) in 2001. Overall, structural differences between upstream and downstream assemblages, and any effects of dam removal, appeared to be small relative to background temporal variability at all sites.

Algae

Chlorophyll *a* concentrations at all sites were significantly lower during Stage 2 than during stages 0 and 1 (there were no significant differences between stages 0 and 1), but the proportionate reduction was significantly greater at downstream (~70%, relative to combined stage 0 and 1 mean) than at upstream (~45%) sites (Tables 2, 4, Fig. 5A). Diatom species richness at downstream sites was ~20% lower during Stage 2 than during stages 0 and 1, with no significant difference between stages 0 and 1. In contrast, richness at the upstream site was higher during stages 1 and 2 than during Stage 0, with no significant difference between stages 1 and 2 (Tables 2, 4, Fig. 5B). Diatom species richness at all sites was very low from April through May of 2001, and increased over summer. Upstream of the dam, richness increased to equal or exceed summer (Stage 0) and autumn (Stage 1) levels, but downstream richness did not (Fig. 5B).

Reduced diatom species richness at downstream sites after dam removal was partly caused by a reduction in the number of rare species. Diatom assemblages at all sites and times were characterized by a few common species and many rare species. Of 158 species identified throughout the study, 6 contributed >50% of all individuals, whereas many species were represented by very few (1–5) individuals. Stage 0 downstream samples averaged 26.3 rare (= those representing <1% of the sample) and 1.5 unique (= found only in that sample) species per sample, compared to 17.4 rare and 0.5 unique species per sample during stage 2. There is no evidence that any species were completely eliminated by the removal event; species that comprised ≥1% in Stage 0 downstream samples were always found after removal.

TABLE 2. Stage means (±1 SE) for macroinvertebrate and algal metrics at upstream and downstream sites. ANOVA results indicate which of Location, Stage, or Location × Stage effects were significant for each metric, followed by comparisons of means. Significant main effects are only indicated if interaction effects were non-significant. Complete ANOVA tables are shown in Tables 3 (macroinvertebrates) and 4 (algae). For algal metrics, Stage 2 means (±1 SE) with spring 2001 samples included are shown in square parentheses. EPT = Ephemeroptera, Plecoptera, and Trichoptera, HBI = Hilsenhoff's Biotic Index. Stages 0, 1, and 2 as in Fig. 2.

Response variable	Location
Macroinvertebrate density (no./m^2)	
	Upstream
	Downstream
Macroinvertebrate taxa richness (no./sample)	
	Upstream
	Downstream
EPT richness (no./sample)	
	Upstream
	Downstream
HBI	
	Upstream
	Downstream
Chlorophyll *a* (mg/m^2)	
	Upstream
	Downstream
Diatom species richness (no./sample)	
	Upstream
	Downstream
Siltation Index	
	Upstream
	Downstream

The average Siltation Index did not vary significantly among stages at downstream sites, but did vary among stages at the upstream site (Tables 2, 4, Fig. 5C). The upstream siltation index was lower during Stage 1 than during stages 0 or 2 (Table 2). Siltation Index values steadily declined at all sites during Stage 0, but this downward trend only continued into Stage 1 at the upstream site (Fig. 5C). The spike in Siltation Index values at downstream sites on the first sample date (~3 wk) after the initial excavation (August 2000, Fig. 4) may reflect a period of high sedimentation. The average Siltation Index increased temporarily at all sites in the spring of 2001, but there were no clear differences between upstream and downstream sites following complete removal (Table 2, Fig. 5C).

There were distinct temporal patterns in the diatom ordination but no separation of upstream and downstream sites at any stage (Fig. 6). Axis 1 reflected a seasonal pattern in the relative abundances of diatom species. Seasonal differences mainly reflected changes in the relative abundances of species that were common throughout the study (*Nitzschia inconspicua*, *Cocconeis placentula*, *Reimeria sinuata*, *Amphora pediculus*) rather than shifts in species composition, although some species were abundant in only one season (e.g., *Gomphonema kobayasii* and *Nitzschia amphibia* in autumn, and *Navicula lanceolata* in spring). Samples collected in summer and autumn of 2001 tended to separate from summer and autumn 2000 samples along Axis 2, with lower scores in 2001 (Fig. 6). Epiphytic species (e.g., *Cocconeis placentula* and *C. pediculus*) were strongly positively correlated with Axis 2, whereas motile species (especially *Nitzschia* and *Navicula* species) were negatively correlated with Axis 2.

TABLE 2. Extended.

Stage			
0	1	2	ANOVA results
			Location × Stage interaction
16,818 (2009)	16,813 (1041)	15,831 (2207)	Stage 0 = Stage 1 = Stage 2
22,913 (4503)	24,537 (957)	8722 (1844)	Stage 0 = Stage 1 > Stage 2
			Location effect
17.1 (2.0)	21.0 (0.2)	19.8 (1.0)	Upstream > Downstream
12.6 (1.6)	18.9 (0.1)	16.7 (2.0)	
			Location effect
8.4 (1.0)	10.8 (0.9)	10.6 (0.7)	Upstream > Downstream
6.7 (1.0)	9.5 (0.3)	8.0 (1.5)	
			Location effect
4.7 (0.3)	4.3 (0.1)	4.4 (0.2)	Upstream < Downstream
5.3 (0.2)	4.7 (0.1)	4.8 (0.2)	
			Site × Stage effect
96.5 (27.1)	144.2 (35.5)	67.1 (12.1) [75.0 (9.0)]	Stage 0 = Stage 1 > Stage 2
187.1 (36.6)	199.9 (43.7)	55.9 (17.9) [73.7 (19.7)]	Stage 0 = Stage 1 ≫ Stage 2
			Site × Stage effect
35.0 (2.2)	43.7 (3.7)	40.2 (1.9) [36.1 (2.6)]	Stage 0 < Stage 1 = Stage 2
43.4 (2.5)	46.3 (3.2)	37.9 (1.4) [34.7 (2.3)]	Stage 0 = Stage 1 > Stage 2
			Site × Stage effect
0.55 (0.03)	0.37 (0.05)	0.51 (0.03) [0.55 (0.05)]	Stage 0 > Stage 1 < Stage 2
0.47 (0.05)	0.46 (0.05)	0.55 (0.04) [0.57 (0.05)]	Stage 0 = Stage 1 = Stage 2

Discussion

A key assumption behind calls to restore rivers by removing dams is that the ecological benefits of dam removal will outweigh the ecological costs. This assumption cannot be fully evaluated without understanding the effects of dam removals on all major components of river ecosystems, both upstream and downstream of dams. Benthic biota downstream of a dam are at particular risk of negative impacts following dam removal because of the potential for impoundment sediments to be transported downstream. We documented significant reductions in macroinvertebrate abundance and diatom richness at downstream sites that persisted for at least 12 mo after dam removal, but observed few changes in these attributes at upstream control sites. Algal biomass also was severely reduced at downstream sites in the year following dam removal, although less severe reductions also occurred upstream of the dam. However, the removal had no detectable effects on the composition or relative abundances of taxa within macroinvertebrate or diatom assemblages.

Removal impacts

The reductions in macroinvertebrate abundance, diatom richness, and algal biomass coincided with, and were probably caused by, the downstream transport of sediments previously stored within the impoundment. Impoundment sediments were carried downstream by flood events in the months following complete removal, causing a substantial reduction in mean par-

TABLE 3. ANOVA results for macroinvertebrate metrics. Format as in Table 1. EPT = Ephemeroptera, Plecoptera, and Trichoptera, HBI = Hilsenhoff's Biotic Index.

		Total density			Number of taxa		
	df	SS	*F*	*p*	SS	*F*	*p*
^{1}Location (6)	1	0.001	0.001	0.982	495.772	18.916	**0.002**
^{2}Stage (5)	2	20.498	2.940	0.110	830.653	2.160	0.178
^{3}Location × Stage (6)	2	12.605	6.056	**0.025**	42.721	0.815	0.476
^{4}Site(L) (8)	2	1.9349	2.372	0.125	42.985	1.823	0.194
^{5}Date(Stage)	8	27.887	14.061	<**0.001**	1538.280	31.499	<**0.001**
^{6}Location × Date(S)	8	8.325	4.198	<**0.001**	209.675	4.293	<**0.001**
^{7}Stage × Site(L) (8)	4	2.005	1.229	0.338	58.696	1.244	0.332
^{8}Site(L) × Date(S)	16	6.526	1.645	0.062	188.665	1.932	**0.020**
^{9}Residual	176	43.384			1074.384		

ticle size that persisted throughout 2001 (Fig. 2; Egan 2001). Deposition of fine sediments generally has negative impacts on benthic communities (Waters 1995, Wood and Armitage 1997), and sediments deliberately or accidentally released from reservoirs can cause pronounced reductions in benthic densities and diversity (Gray and Ward 1982, Marchant 1989, Doeg and Koehn 1994).

It is possible that some of the apparent impacts on downstream benthic assemblages were caused directly by the floods in Stage 2, including the large December 2000 event, rather than by dam removal. For example, reductions in algal biomass observed at all sites in Stage 2 may have been caused by increased frequency of scouring flows. Floods affected all sites, however, whereas persistent reductions in macroinvertebrate density and diatom richness were only observed downstream of the dam, providing evidence of substantial dam removal effects. We cannot separate completely dam removal effects from flood effects because these factors interacted, as will often be the case. A major effect of dam removal is downstream sedimentation, and sediment can only be transported downstream by flows of sufficient power.

A possible alternative explanation for the observed results is that flooding differentially impacted upstream and downstream sites for reasons unrelated to the dam removal. This explanation is unlikely for a number of reasons. First, macroinvertebrate and algal assemblages at upstream and downstream sites had similar taxonomic compositions, so they would be expected to have similar responses to floods. Downstream sites did have proportionately more chironomids than upstream sites, but chironomids generally recover rapidly after floods (Thomson 2002), so this initial difference is unlikely to explain the persistent difference in macroinvertebrate densities between upstream and downstream sites for 12 mo after removal. Second, there is no evidence that smaller floods throughout 2001 differentially impacted upstream and downstream assemblages (Figs 3, 5). Last, a 66.3 m^3/s flood (larger than the 47.9 m^3/s December 2000 flood) occurred in March 2000 (USGS hydrographic data), but there is no evidence that this flood had persistent, differential impacts on upstream and downstream assemblages: macroinvertebrate densities, algal biomass, and diatom richness were all at least as high at downstream sites as at upstream sites within 3 mo of that event (i.e., by June 2000; Figs 3, 5).

The 2-stage removal process made it easier to distinguish among alternative explanations for the biotic responses to dam removal that we observed. The first stage of the removal eliminated the impoundment, but the remaining dam footing minimized downstream sediment transport (at least under the flow conditions prevalent during Stage 1). We observed very few biological changes at downstream sites during this stage, suggesting that changes in water quality following the impoundment's elimination were not a major factor affecting benthic organisms. This inference is supported by results of a concurrent study that found negligible water-quality effects of the dam or its removal (Bushaw-Newton et al. 2002). In contrast, marked effects on both algae and macroinvertebrates occurred after the Stage 2 removal, when downstream sediment transport increased dramatically.

TABLE 3. Extended.

Number of EPT taxa			HBI		
SS	*F*	*p*	SS	*F*	*p*
165.525	19.400	**0.002**	11.789	38.976	**<0.001**
234.854	1.279	0.330	8.752	1.489	0.282
14.590	0.855	0.461	0.497	0.822	0.474
4.533	0.663	0.529	0.886	11.781	**<0.001**
734.678	32.628	**<0.001**	23.509	78.186	**<0.001**
68.259	3.032	**0.003**	2.420	8.048	**<0.001**
15.048	1.101	0.390	1.159	2.815	0.061
54.656	1.214	0.261	1.647	2.739	**0.001**
495.364			6.615		

Possible long-term effects of dam removal

Theory suggests that increased downstream sediment deposition will continue until a relatively stable channel and floodplain have developed above the former dam, after which particle sizes in downstream reaches will gradually increase as excess fine sediment decays (Pizzuto 2002). Macroinvertebrate and algal assemblages in riffles downstream of the dam are likely to recovery rapidly once fine sediment loads are reduced (Gray and Ward 1982, Marchant 1989, Doeg and Koehn 1994, Wood and Armitage 1997), especially given that species composition was largely unaffected for both groups. Geomorphic responses to dam removal remain poorly understood, however, and recovery rates are difficult to predict. Surveys downstream of the dam during 2004 suggest that bed sediments are yet to recover from the effects of dam removal (J. Pizzuto, University of Delaware, personal communication), and that sediment transport and deposition are continuing to have adverse effects on fish assemblages (R. J. Horwitz, Patrick Center for Environmental Research, personal communication). These results suggest that geomorphic adjustment, and therefore biological recovery, following small dam removal could take many years. This observation underscores the need for additional studies that quantify ecological responses to dam removal over longer time spans.

An important question is whether removal will have any positive long-term effects in downstream reaches, assuming that the negative impacts of sedimentation eventually dissipate. Prior to dam removal, sites downstream of the dam were sometimes characterized by nuisance algal growth (biomass >200 mg/m chlorophyll *a*) and consistently had poorer HBI scores, lower macroinvertebrate richness (especially in EPT taxa), and proportionately more chironomids than upstream sites (Figs 3, 5). Although algal biomass was lower after dam removal, there was no evidence of improvement in macroinvertebrate metrics up to 1 y after removal. The depauperate macroinvertebrate assemblages and higher algal biomass at downstream sites relative to upstream sites prior to dam removal probably reflect the greater urban inputs and reduced riparian vegetation downstream of the dam. It is unlikely that dam removal alone will cause a substantial improvement in downstream ecological integrity because the Manatawny dam had minimal downstream effects on water quality (Bushaw-Newton et al. 2002), and urban impacts continue unabated. The reduction in algal biomass most likely reflects the combined effects of floods and sedimentation, and may not be indicative of any longer-term effect of dam removal on primary production.

Implications for dam removal as a restoration method

In the context of restoration, the downstream effects of removing the Manatawny dam are unlikely to have serious implications. The structure of macroinvertebrate and algal assemblages was largely unaffected, and abundances are likely to recover rapidly once fine sediment loads are reduced in downstream riffles. Stanley et al.

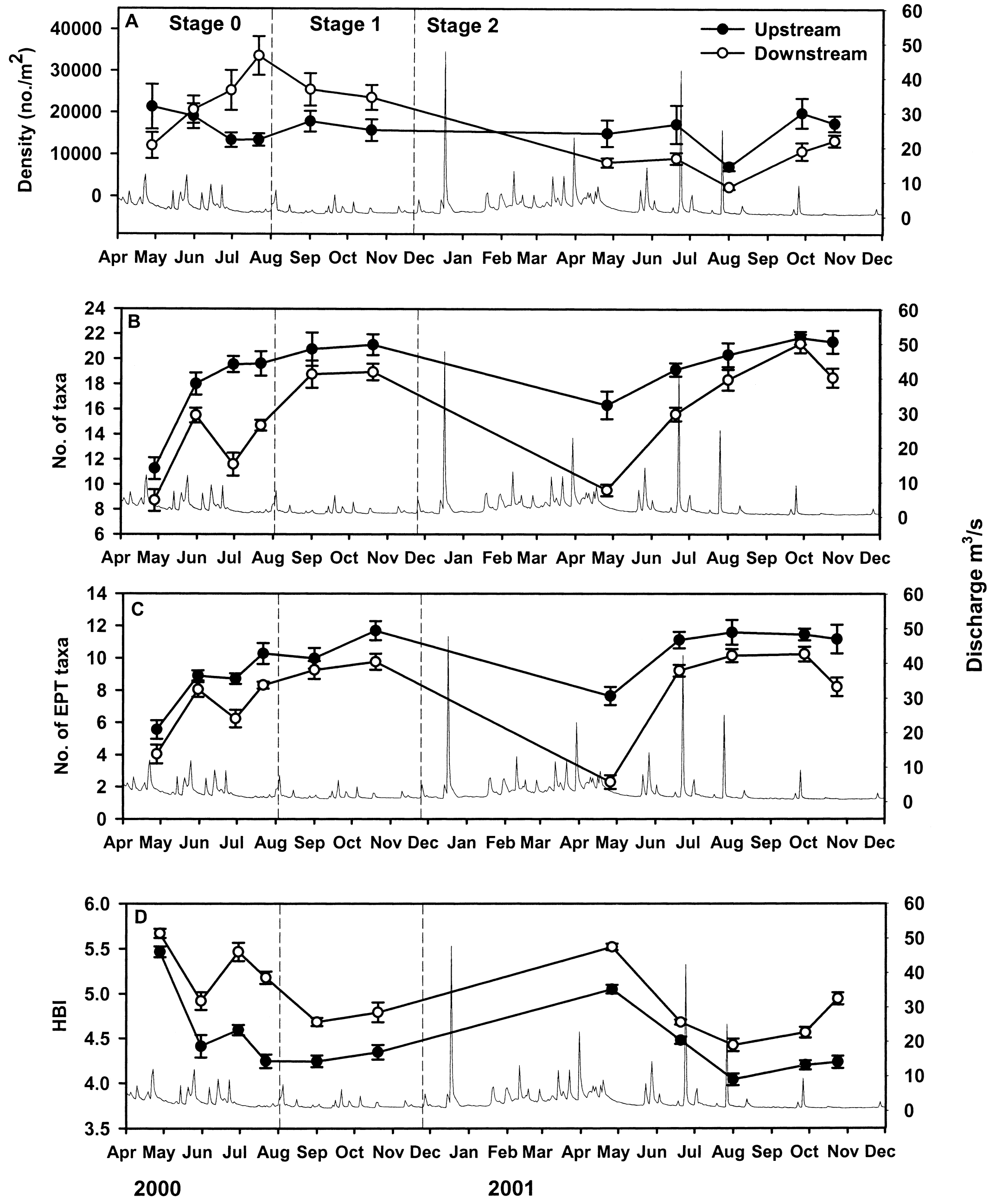

FIG. 3. Changes in total macroinvertebrate density (A), total taxa richness (B), Ephemeroptera, Plectoptera and Trichoptera (EPT) taxa richness (C), and Hilsenhoff's Biotic Index (HBI) (D), at upstream and downstream sites over the study period. Points are location means (±1 SE, $n = 2$ sites per location). Stages and hydrograph as in Fig. 2.

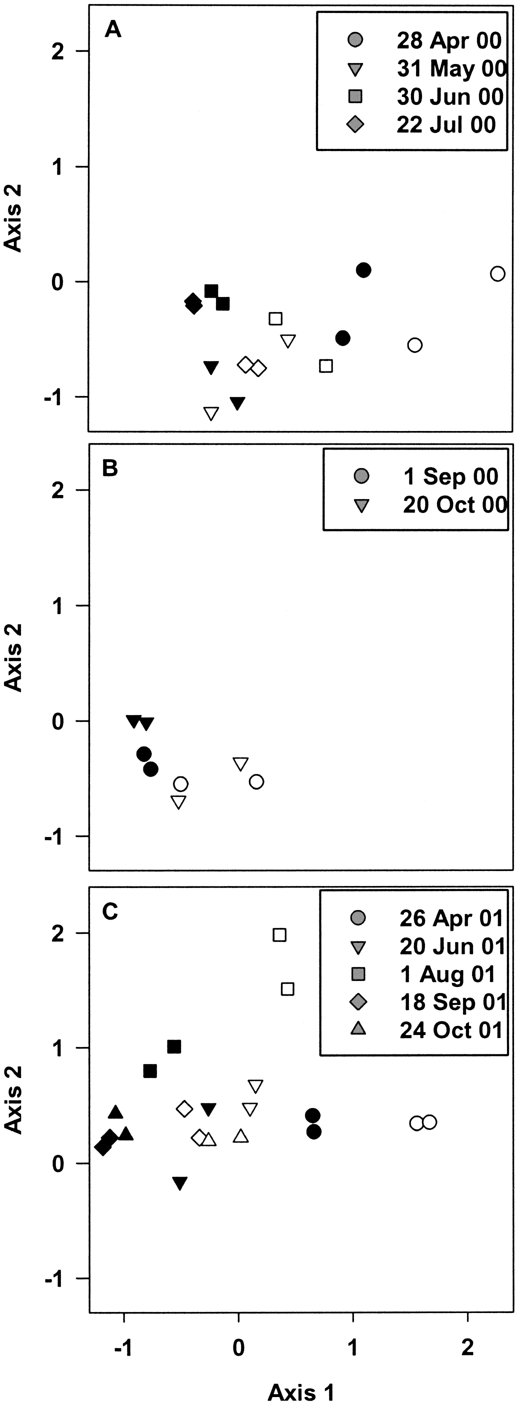

FIG. 4. Nonmetric Multidimensional Scaling (NMDS) ordination of macroinvertebrate assemblages at sites upstream (solid symbols) and downstream (open symbols) of the dam throughout the study. Symbol shape indicates sample date. Each stage is plotted on a separate panel (a single ordination was performed). A.—Pre-removal stage (0). B.—Partial removal stage (1). C.—Post-removal stage (2). Ordination stress = 0.18.

(2002) also found no change in macroinvertebrate assemblage structure or condition metrics following dam removals in a Wisconsin river. These results, and observations that even severely depleted benthic assemblages often recover rapidly once sediments released from reservoirs are flushed from the system (Gray and Ward 1982, Doeg and Koehn 1994, Stanley and Doyle 2003), suggest that small dam removals are unlikely to have long-term deleterious impacts on downstream benthic communities as long as highly vulnerable species (e.g., endangered freshwater mussels; see Sethi et al. 2004) are not at risk. If downstream effects are ecologically neutral in the long-term, then small dam removals will often have a net ecological benefit. That is, the long-term benefits associated with the reconnection of downstream and upstream reaches and the restoration of lotic habitats in the former impoundment (Stanford et al. 1986, Bednarek 2001, Stanley et al. 2002) will often outweigh the relatively short-term ecological impacts of downstream sedimentation following removal.

Acknowledgements

Funding for this project was provided by a Growing Greener Grant from the Pennsylvania Department of Environmental Protection (PA DEP), an anonymous foundation, and the Patrick Center's Endowment for Innovative Research. The views expressed herein do not necessarily reflect those of PA DEP. We thank our many colleagues in the Patrick Center's Institute for Watershed Restoration for their help with study design, data collection and interpretation, especially Karen Bushaw-Newton, Erin Hagan, Richard Horwitz, Tom Johnson, Roger Thomas, and David Velinsky. Jim Pizzuto and Jennifer Egan (University of Delaware) generously shared the results of their geomorphic studies, and Scott Carney (Pennsylvania Fish and Boat Commission) offered valuable advice and assistance throughout the project. This manuscript benefited greatly from the constructive com-

TABLE 4. ANOVA results for algal metrics. Format as in Table 1.

		Number of taxa			Chlorophyll *a*			Siltation Index		
	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
[1]Site	2	0.039	1.627	0.224	0.591	1.446	0.267	0.008	0.258	0.775
[2]Stage (4)	2	0.149	2.698	0.121	12.768	4.951	**0.035**	0.103	0.597	0.571
[3]Site × Stage	4	0.159	3.323	**0.033**	2.915	3.565	**0.027**	0.225	3.667	**0.024**
Site$_{\text{down}}$ × Stage	2	0.050	2.070	0.155	0.906	2.220	0.137	0.048	1.595	0.230
Site$_{\text{down vs up}}$ × Stage	2	0.109	4.542	**0.025**	2.009	4.923	**0.020**	0.177	5.913	**0.011**
[4]Date(Stage)[a]	9	0.249	2.325	0.061	11.604	6.308	**<0.001**	0.776	5.624	**0.001**
[5]Residual[a]	18	0.215			3.679			0.276		

[a] Residual error includes error from intestable Site × Date(S) term. *F*-test for term 4 assumes this component is 0

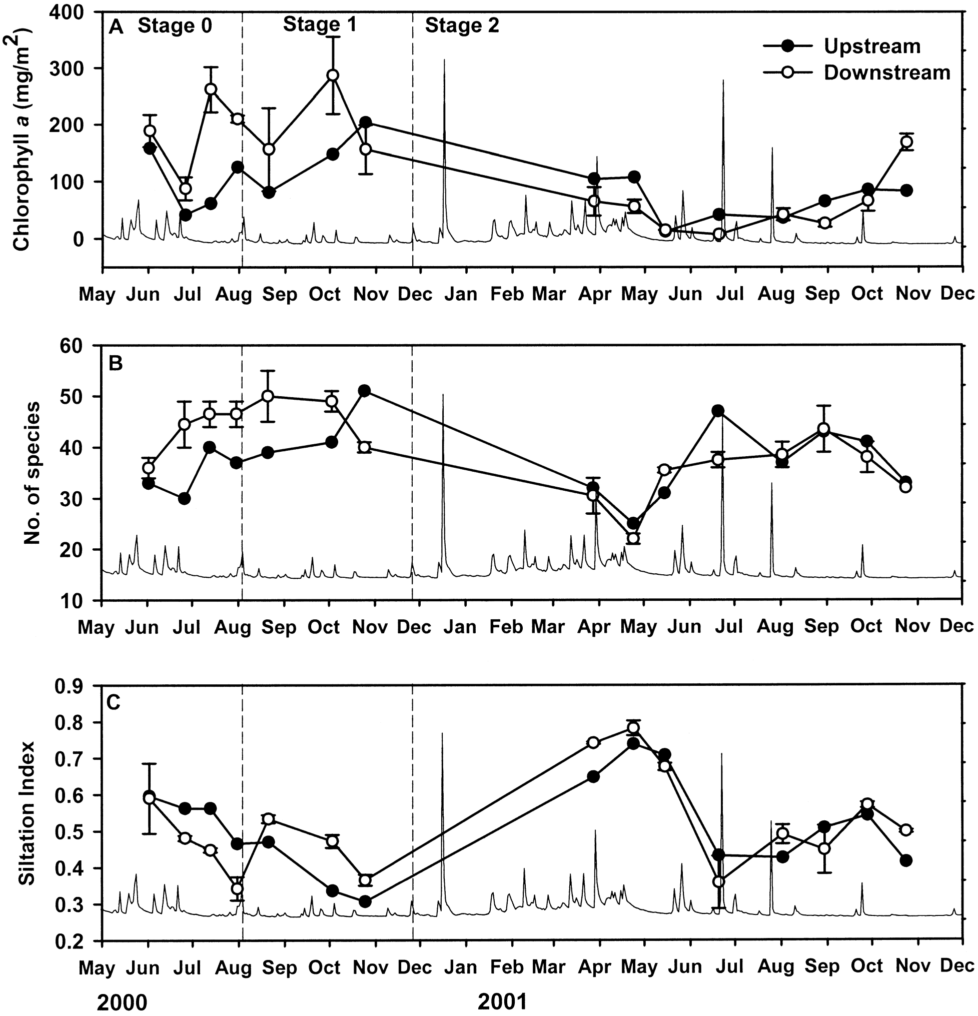

FIG. 5. Changes in chlorophyll *a* concentrations (A), species richness (B), and diatom-based Siltation Index (C) at upstream and downstream sites over the study period. Points are location means (±1 SE, n = 2 sites for downstream and 1 site for upstream). Stages and hydrograph as in Fig. 2.

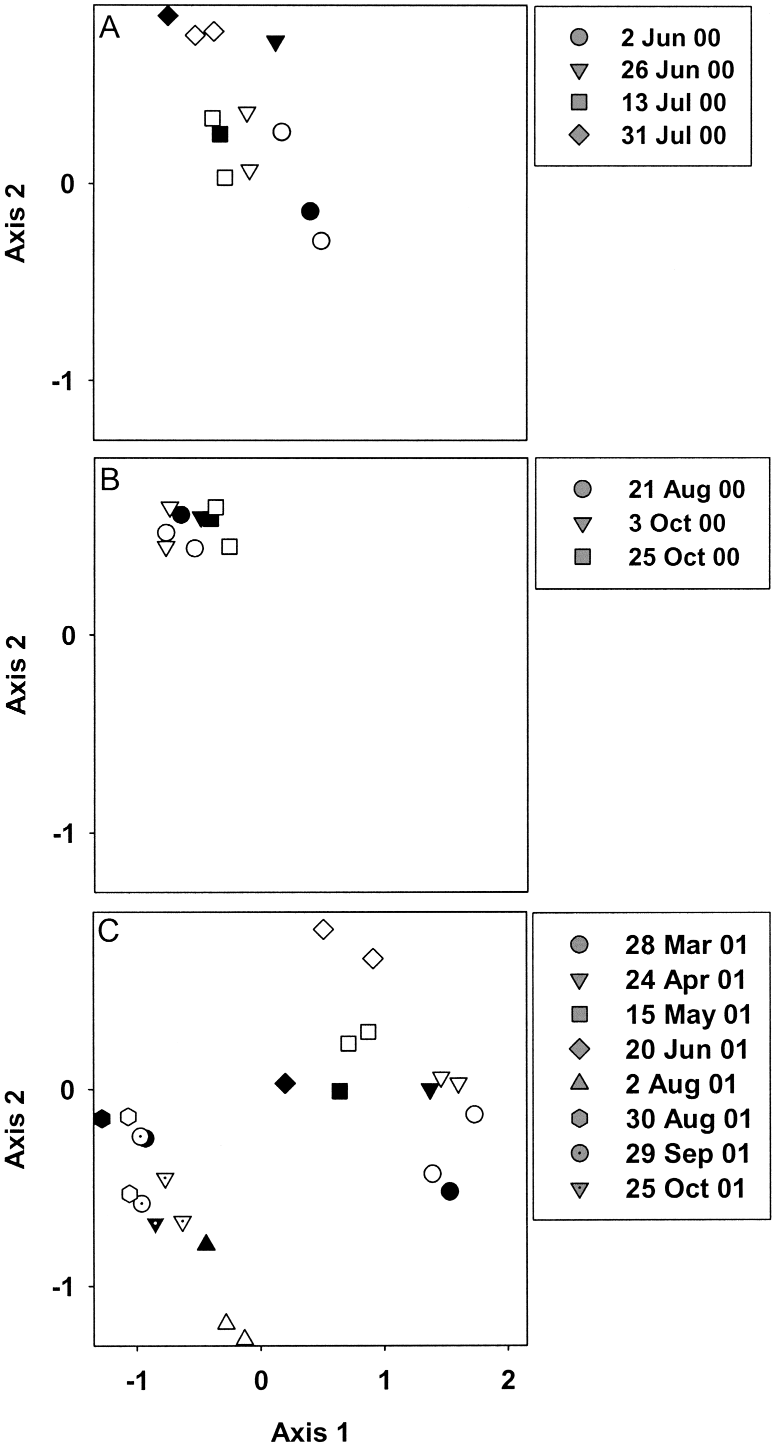

FIG. 6. Nonmetric Multidimensional Scaling (NMDS) ordination of diatom assemblages at sites upstream (solid symbols) and downstream (open symbols) of the dam throughout the study. Format as in Fig. 4. Ordination stress = 0.14.

ments of Scott Larned, David Rosenberg, and 2 anonymous reviewers.

Literature Cited

APHA (AMERICAN PUBLIC HEALTH ASSOCIATION). 1995. Standard methods for the examination of water and wastewater. 19th edition. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, DC.

BAHLS, L. R., R. BUKANTIS, AND S. TRALLES. 1992. Benchmark biology of Montana reference streams. Water Quality Bureau, Montana Department of Health and Environmental Science, Helena, Montana. (Available from: http://www.deq.state.mt.us/wqinfo/monitoring/Publications/bench_bio_of_mt.asp)

BARBOUR, M. T., J. GERRITSEN, B. D. SNYDER, AND J. B. STRIBLING. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, 2nd edition. EPA 841-B-99-002. Office of Water, US Environmental Protection Agency, Washington, DC.

BEDNAREK, A. T. 2001. Undamming rivers: a review of the ecological impacts of dam removal. Environmental Management 27:803–814.

BUSHAW-NEWTON, K. L., D. D. HART, J. E. PIZZUTO, J. R. THOMSON, J. E. EGAN, J. T. ASHLEY, T. E. JOHNSON, R. J. HORWITZ, M. KEELEY, J. LAWRENCE, D. CHARLES, C. GATENBY, D. A. KREEGER, T. NIGHTENGALE, R. L. THOMAS, AND D. J. VELINSKY. 2002. An integrative approach towards understanding ecological responses to dam removal: the Manatawny Creek study. Journal of the American Water Resources Association 38:1581–1599.

CHANCELLOR, P. 1953. A history of Pottstown, Pennsylvania. Historical Society of Pottstown, Pottstown, Pennsylvania.

CHARLES, D. F., C. KNOWLES, AND R. DAVIS. 2002. Protocols for the analysis of algal samples collected as part of the U. S. Geological Survey National Water-Quality Assessment Program. Report No. 02-06. Patrick Center for Environmental Sciences, The Academy of Natural Sciences, Philadelphia, Pennsylvania. (Available from: http://diatom.acnatsci.org/nawqa/pdfs/ProtocolPublication.pdf)

CLARKE, K. R., AND R. M. WARWICK. 1994. Change in marine communities: an approach to statistical analysis and interpretation. 1st edition. Plymouth Marine Laboratory, Natural Environment Research Council, Plymouth, UK.

DOEG, T. J., AND J. D. KOEHN. 1994. Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. Regulated Rivers: Research and Management 9:263–277.

EGAN, J. M. 2001. Geomorphic effects of dam removal on the Manatawny Creek, Pottstown, Pennsylvania. MSc thesis, University of Delaware, Newark, Delaware.

ENNIS, G. L., AND L. J. ALBRIGHT. 1982. Distribution and abundance of periphyton and phytoplankton species in two Subarctic Canadian rivers. Canadian Journal of Botany 60:224–236.

GRAY, L. J., AND J. V. WARD. 1982. Effects of sediment releases from a reservoir on stream macroinvertebrates. Hydrobiologia 96:177–184.

GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York.

HART, D. D., T. E. JOHNSON, K. L. BUSHAW-NEWTON, R. J. HORWITZ, A. T. BEDNAREK, D. F. CHARLES, D. A. KREEGER, AND D. J. VELINSKY. 2002. Dam removal: challenges and opportunities for ecological research and river restoration. BioScience 52: 669–681.

HILSENHOFF, W. L. 1987. An improved biotic index of organic stream pollution. Great Lakes Entomologist 20:31–39.

JACCARD, J. 1998. Interaction effects in factorial analysis of variance. Sage University Papers Series on Quantitative Applications in the Social Sciences, 07-118. Sage, Thousand Oaks, California.

KRAMMER, K., AND H. LANGE-BERTALOT. 1986–1991. Bacillariophyceae. Teil 1–4 *in* H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer (editors). Süsswasserflora von Mitteleuropa. Gustav Fischer Verlag, Stuttgart, Germany.

MARCHANT, R. 1989. Changes in the benthic invertebrate communities of the Thomson River, southeastern Australia, after dam construction. Regulated Rivers: Research and Management 4:71–89.

PATRICK, R., AND C. W. REIMER. 1966. The diatoms of the United States (exclusive of Alaska and Hawaii). Volume 1: Systematic descriptions of diatoms of the taxonomic orders Fragilariales, Eunotiales, Achnanthales, and Navicuales (family Naviculaceae). Monograph 13, Volume 1. The Academy of Natural Sciences, Philadelphia, Pennsylvania.

PATRICK, R., AND C. W. REIMER. 1975. The diatoms of the United States (exclusive of Alaska and Hawaii). Volume 2: Systematic descriptions of diatoms of the taxonomic orders Navicuales (families Entomoneidaceae, Cymbellaceae, and Gomphonemaceae), and Epithemiales Monograph 13. Volume 2. The Academy of Natural Sciences, Philadelphia, Pennsylvania.

PETTS, G. E. 1984. Impounded rivers: perspectives for ecological management. John Wiley and Sons, New York.

PIZZUTO, J. 2002. Effects of dam removal on river form and process. BioScience 52:683–691.

POFF, N. L., J. D. ALLAN, M. B. BAIN, J. R. KARR, K. L. PRESTEGAARD, B. D. RICHTER, R. E. SPARKS, AND J. C. STROMBERG. 1997. The natural flow regime:

a paradigm for conservation and restoration of river ecosystems. BioScience 52:659–668.

POFF, N. L., AND D. D. HART. 2002. How dams vary and why it matters for the emerging science of dam removal. BioScience 52:659–668.

QUINN, G. P., AND M. J. KEOUGH. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

SETHI, S. A., A. R. SELLE, M. W. DOYLE, E. H. STANLEY, AND H. E. KITCHEL. 2004. Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin (USA). Hydrobiologia 525:157–165.

SHUMAN, J. R. 1995. Environmental considerations for assessing dam removal alternatives for river restoration. Regulated Rivers: Research and Management 11:249–261.

STANFORD, J. A., J. V. WARD, W. J. LISS, C. A. FRISSELL, R. N. WILLIAMS, J. A. LICHATOWICH, AND C. C. COUTANT. 1986. A general protocol for restoration of regulated rivers. Regulated Rivers: Research and Management 12:391–413.

STANLEY, E. H., AND M. W. DOYLE. 2003. Trading off: the ecological effects of dam removal. Frontiers in Ecology and the Environment 1:15–22.

STANLEY, E. H., M. A. LUEBKE, M. W. DOYLE, AND D. W. MARSHALL. 2002. Short-term changes in channel form and macroinvertebrate communities following low-head dam removal. Journal of the North American Benthological Society 21:172–187.

THOMSON, J. R. 2002. The effects of hydrological disturbance on the densities of macroinvertebrate predators and their prey in a coastal stream. Freshwater Biology 47:1333–1351.

UNDERWOOD, A. J. 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. Australian Journal of Marine and Freshwater Research 42:569–588.

UNDERWOOD, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications 4:3–15.

WALSH, C. J. 1997. A multivariate method for determining optimal subsample size in the analysis of macroinvertebrate samples. Marine and Freshwater Research 48:241–248.

WARD, J. V., AND J. A. STANFORD. 1979. The ecology of regulated streams. Plenum Publishing, New York.

WATERS, T. F. 1995. Sediment in streams: sources, biological effects and control. American Fisheries Society Monograph 7. American Fisheries Society, Bethesda, Maryland.

WOOD, P. J., AND P. D. ARMITAGE. 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21:203–217.

Received: 7 July 2003
Accepted: 20 November 2004