

**Running head: Impacts of dam removal on downstream benthic assemblages**

**The effects of removing a small dam on benthic macroinvertebrate and algal assemblages in a Pennsylvania stream.**

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## Abstract

Dam removal is seen increasingly as a viable method of restoring 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 removal of a small, run-of-river dam on Manatawny Ck, Pennsylvania. Benthic macroinvertebrates, algae, and habitat characteristics were monitored upstream and downstream of the dam for 4 months before and 12 months after dam removal, as well as for 3 intermediate months when only half of the dam structure had been removed (i.e. the impoundment was largely eliminated but sediment remained trapped behind the remaining structure). Macroinvertebrate density, algal biomass, and diatom species richness were significantly reduced following complete dam removal, but overall assemblage structure (as indicated by NMDS ordinations) remained similar to upstream control sites throughout the study for both taxonomic groups. Downstream impacts occurred only after the dam structure had been completely removed and sediments had been transported into downstream reaches by high flow events, causing significant fining of riffle substrata. Biotic impacts generally persisted for the duration of the study (12 months after removal), but are expected to dissipate once sediments are transported farther downstream. Together with results of other studies of dam removals and sediment releases, our results suggest that downstream sedimentation following dam removals will often cause reductions in benthic densities and may also reduce benthic diversity, but for small dams such impacts may be relatively minor and will usually be temporary.

## Introduction

Dam removal is a relatively new and potentially important method of restoring ecological integrity to rivers and streams. Dams impede the flux of water, sediments, biota and nutrients, and can fundamentally change the structure and dynamics of upstream and downstream aquatic and riparian habitats and associated biotic communities (Ward and Stanford 1979, Petts 1984, Poff et al. 1997). Increasing awareness of the ecological impacts of dams, combined with the rising financial costs of maintaining aging or obsolete structures, has led to increasing calls for dam removals. In the United States, over 500 dams have been removed in the past century, with the rate of removal increasing rapidly over the past two decades, and expected to increase further in coming years (Poff and Hart 2002, Stanley and Doyle 2003).

Understanding the potential ecological costs and benefits of removing dams is essential to making informed decisions about whether and how a particular dam should be removed (Hart et al. 2002). Presently, however, there is little empirical data on which to base predictions about ecological responses to dam removal. Less than 5% (approximately 20) of all dam removals in the United States have been accompanied by published ecological studies (Hart et al. 2002), and these are often limited in scope. Most concentrate on impacts on fish and /or focus on changes in the former 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 no studies have evaluated algal responses.

Most dams that have been removed were relatively small structures (usually less than 5 m high), and small dams will probably continue to be removed at a greater rate than large dams. Small dams (< 5m high) 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 cheaper to remove (Poff and Hart 2002). Despite their abundance, the ecological impacts of small dams are less well documented than those of large dams (Hart et al. 2002). This makes assessing the likely benefits of removing small dams particularly difficult. The putative benefits of dam removal include the restoration of free-flowing habitat to impounded reaches, restored longitudinal connectivity, and restoration of natural flow and thermal regimes to downstream reaches (Stanford et al. 1986, Bednarek 2001, Stanley et al. 2002). Removing small dams can improve

fish passage, and will restore lotic habit within the former impoundment (Bushaw-Newton et al. 2002, Stanley et al. 2002). Less is known, however, about the impacts of small dams on water quality, sediment flux, flow regimes, and temperatures. For example, removal of a low-head, run-of-river dam that has a short hydraulic residence time and a limited storage volume may not improve downstream water quality, thermal dynamics, or flow regimes.

The ecological risks of removing small dams may also be relatively low. The most frequently cited ecological risk of removing dams is the downstream transport of sediments previously stored in impoundments (Shuman 1995, Bednarek 2001, Poff and Hart 2002, Bednarek 2002). The volumes of sediment stored behind small dams may be small, however, and may be rapidly flushed downstream, depending on flow regimes. Nevertheless, sedimentation can severely impact all trophic groups (Waters 1995, Wood and Armitage 1997), especially benthic organisms that may be critical resources for fish populations – the usual foci of restoration efforts.

The aim of this study was to investigate the impacts of removing a small dam on downstream assemblages of benthic algae and macroinvertebrates. Although the physical disturbance associated with dam excavation is likely to have short-term (e.g., several weeks) impacts, it is less clear whether these effects last long enough (e.g., months to years) to substantially impact ecological characteristics or, to necessitate modification of restoration strategies. Thus, the specific aim of our study was to determine whether there were any negative or positive downstream effects of dam removal that persisted for at least 12 months. We examined changes in macroinvertebrate and algal abundance and assemblage composition, in order to assess the medium-term impact of the removal on these critical components of the stream ecosystem. The impacts of dam removal on key aspects of benthic habitat (i.e. substrate particle size and hydraulic characteristics) were also investigated.

## Methods

### Study Site and Sampling Design

The study was conducted in the lower reaches of Manatawny Creek, a fourth-order stream in the piedmont physiographic province near Pottstown in southeastern PA (Figure 1). Manatawny Creek has a drainage area of 238.3 km<sup>2</sup>, of which approximately 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 (shale and schist) and was approximately 2 m high, 2 m thick and 30 m across. Water was impounded for approximately 500 m upstream, with a hydraulic residence time at base flow of 1-2 hrs. The mean annual flow in the dam area is 3.7 m<sup>3</sup>s<sup>-1</sup>, and the highest recorded flow from 1975 through 2000 was 200 m<sup>3</sup>s<sup>-1</sup>.

The dam was removed in a 2-stage process in 2000 (see Bushaw-Newton et al. 2002 for further details). Following the initial excavation in August 2000, geomorphic surveys conducted in early autumn revealed that only about half of the structure's 2 m height 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). The rest of the dam was removed in late November, 2000. Therefore, we defined sampling dates as pre-removal (Stage 0), partial removal (Stage 1), and complete removal (Stage 2). One potential benefit of the 2-stage removal process is that it provided an opportunity to examine the ecological consequences of increased longitudinal connectivity and possible improvements in water quality stemming from impoundment draw-down without the potentially confounding effects of marked increases in downstream sedimentation. On the other hand, this unplanned, 2-stage removal process complicated the sampling design. For example, samples collected after the first excavation were originally intended to serve as post-removal data, but actually represented "partial removal" data. Furthermore, evidence of potential short-term ecological responses to the complete removal (November 2000) would have required benthic sampling during winter, when abiotic and biotic conditions are markedly different from those during the warmer seasons (summer and autumn) when most of our pre-removal sampling was conducted. This large seasonal difference would have

greatly complicated any attempt to discern a short-term ecological response to dam removal (Underwood 1991). Finally, a large December flood caused considerable scouring (authors' personal observations) and likely reduced abundances of benthic organisms, and the increased temporal variation caused by this natural disturbance would have further limited our ability to detect any short-term removal impacts. For these reasons, we chose not to sample over the winter immediately following dam removal, but to concentrate on the medium-term impacts of removal by sampling principally in summer and autumn, a period for which we had comparable pre-removal samples. Our sampling design therefore specifically addresses ecological impacts of removal that persist for ~ 12 months, which is an important time span for evaluating restoration outcomes.

A modified Before-After-Control-Impact approach (BACI, Green 1979, Downes et al. 2002) was used to study how macroinvertebrate and algal assemblages located in riffles downstream of the impoundment responded to dam removal. Macroinvertebrates and benthic algae were sampled multiple times during each of the three stages at downstream impact and upstream control sites. Macroinvertebrates were sampled at two upstream control sites (Sites 1 and 2, 2.0 and 2.2 km upstream from the dam respectively) and two downstream "impact" sites (Sites 3 & 4, 0.15 and 0.28 km downstream of the dam respectively). Algae were sampled at one upstream (Site 1) and two downstream (Sites 3 & 4) sites. Samples were collected four times prior to dam removal (Stage 0) for both groups, two (macroinvertebrates) and three (algae) times during Stage 1, and five (macroinvertebrate) and eight (algae) times after complete removal (Stage 2). All sites were riffle habitats (23-45 m long, ~12 m wide) with similar flow and substrate characteristics.

#### Macroinvertebrate and habitat sampling

Five Surber samples (area = 0.093 m<sup>2</sup>, mesh = 500 µm) were collected at each site on each date. Samples were preserved in 95% ethanol. Mean water velocity directly above the bed and mean depth were measured at each sample location prior to collection. Velocity was measured with a Marsh-McBirney flowmeter for 30 seconds. The proportion of substrate elements falling into each of 5 size classes (boulder >256mm, cobble 64-256 mm, pebble 16-64 mm, gravel 2-16 mm, sand 0.063-2 mm) was visually estimated for each sampled area (Minshall 1984).

In the laboratory, macroinvertebrate samples were subsampled using a ten-cell sample splitter until at least 100 animals had been counted from each sample. Insects other than Chironomidae (family) were identified to genus, 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 riffle were sampled for periphytic algae at approximately monthly intervals. Rock surfaces were scrubbed vigorously with a brush (or sharp implement for well attached filamentous algae) to remove all filamentous and surface films of algae. Rock samples were composited into single samples 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 tracing the general outline of the rock onto waterproof paper and by creating an aluminium foil mold (Ennis and Albright 1982, Aloï 1990). Areas of outlines and foil molds 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 and ash-free dry mass (AFDM) were determined using standard methods (APHA, AWWA and WPCF, 1995; U.S. EPA, 1992).

#### Diatom identification and enumeration

Counts of 500 frustules/1000 valves were conducted for each sample using a Zeiss Axioskop at 1000x 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 1986-91).

#### Data analyses

A combination of univariate analyses of community metrics and multivariate ordinations was used to examine macroinvertebrate and algal responses to dam removal.

Univariate Analyses:-Repeated measures 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, Barbour et al. 1999), 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  
5 standardized to the number of (EPT) 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 calculated).

For macroinvertebrates, a four factor ANOVA model was used with Location (upstream and downstream) and Stage (pre-removal, stage 1, and stage 2) as fully crossed, fixed factors, with significant  
10 Stage×Location interactions indicating possible dam removal effects (Underwood 1991, Downes et al 2002). Date was a random factor nested in Stage and Site a fixed factor nested in Location. Pairwise comparisons of significant main effects means (if no interaction) or simple main effects tests (if interaction - means of Factor A compared within each level of Factor B and vice-versa, Quinn and Keough 2002) were conducted as t-tests using variance estimates and degrees of freedom derived from  
15 appropriate (=  $F$ -ratio denominator) 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, rather 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  
20 only (Site<sub>down</sub> × Stage). If the Site<sub>down</sub> × Stage term was non-significant, the (consistent) temporal pattern at downstream sites was compared to the temporal pattern at the upstream control site by testing a Site<sub>down</sub> v Site<sub>up</sub> × Stage term, and by conducting simple main effects tests on upstream and combined downstream means. Algal samples collected in Spring 2001 (i.e. 1<sup>st</sup> 3 post-removal samples) were not included in ANOVA because no pre-removal spring samples were collected (see ordination results for large seasonal  
25 variability) and their inclusion would have created a very unbalanced design.

Hydraulic variables and mean particle size ( $\phi$ ) were analyzed using the same ANOVA model as that used for macroinvertebrate metrics.

Assumptions of normality and variance homogeneity were checked with box and residual plots and appropriate diagnostic tests, and were always met by either raw or log transformed data. Metrics were also analyzed with separate, balanced ANOVA designs comparing pre-removal scores to either stage 1 or stage 2, randomly omitting dates as appropriate to create balanced designs. Results of these analyses did not differ (in terms of acceptance or rejection of null hypotheses) from those of full analyses and are not presented.

Multivariate analyses:-Changes in macroinvertebrate and diatom assemblage structure (i.e. the species present and their relative abundances) following dam removal were examined with Nonmetric Multi-Dimensional Scaling (NMDS) ordinations (Clarke and Warwick 1994) using Bray-Curtis similarity matrices derived from square root transformed data. Separate ordinations were performed on the complete macroinvertebrate data, with all Surber samples included as separate samples, and on aggregated data, with composite samples created for each site on each date. While patterns from both ordinations were similar, combining samples from the same site and date produced a lower stress value (0.18 vs 0.23 for 2 dimensions) and only this ordination is presented. All diatom samples were included in a single NMDS.

The NMDS axis scores were correlated with (square root transformed) counts of each taxon to determine which taxa may have contributed most to the distribution of samples in ordination space. In addition, the SIMPER routine in Primer was used to identify the (square root transformed) taxa that most contributed to differences among locations (macroinvertebrates) or sites (diatoms) within each stage.

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## Results

### Macroinvertebrates

There was a significant Location  $\times$  Stage interaction for the total density of macroinvertebrates (Table 1). Macroinvertebrate density was significantly lower at downstream sites after complete removal (i.e. throughout stage 2) than during pre-removal or partial removal stages, but remained relatively constant at upstream sites (Table 1, Figure 2). Location  $\times$  Stage interactions were non-significant for all other macroinvertebrate metrics. HBI scores for all sites generally fell within the “Good” range ( $<5.5$ ), but were consistently higher (higher pollution tolerance) for downstream than upstream sites. Downstream sites also tended to have lower taxonomic diversity, especially in EPT taxa (Table 1, Figure 2), than upstream sites. These differences remained throughout the study period, and were apparently unaffected by dam removal.

The macroinvertebrate NMDS ordination (Figure 3) indicated a seasonal trend along the first (horizontal) axis, with sites moving from right to left from spring through fall in both years. This pattern was consistent at upstream and downstream sites, but on any date, downstream sites had higher axis 1 scores than upstream sites. The seasonal pattern reflects summer (e.g. *Hydropsychidae*, *Baetis*, *Acentrella*, *Serratella*, *Simuliidae*) or fall (e.g. *Optioservus*, *Cheumatopsyche* and *Planariidae*) density peaks. The consistent separation of upstream and downstream sites along the first axis mainly reflects higher chironomid and lower *Optioservus* densities at downstream sites. Other taxa, such as *Hydropsyche*, *Cheumatopsyche*, *Serratella* and *Stenelmis*, periodically had higher densities at upstream than downstream sites. The separation of upstream and downstream sites along the first axis did not change after either removal event. The second axis was most strongly (negatively) correlated with chironomid densities, and there was a general trend for all sites to move up this axis with time, mainly reflecting lower chironomid densities in 2001, as well as lower densities of other common taxa (*Prosimulium*, *Hydrachnida*, *Serratella*, *Oligochaeta*, *Tricorythodes*, *Stenonema*) and higher Nematoda densities. 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

Both chlorophyll-a and diatom species richness (Figure 4) were significantly lower at downstream sites in the summer and autumn after complete removal than in the corresponding pre-removal period, while showing less severe reductions (chlorophyll-a) or no change (richness) at the upstream control site (Table 2). Richness values were particularly low at all sites from April through May of 2001 (a possible seasonal effect), and increased over summer (as they had in 2000). Upstream richness recovered fully to levels observed in summer and autumn of 2000, but downstream richness did not. Chlorophyll-a and species richness were generally higher downstream than upstream prior to removal, so the post-removal reductions resulted in similar values at all sites in 2001 (Figure 4).

The lower species richness at downstream sites (Figure 4) after removal was largely driven 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 more than 50% of all individuals, while many species were represented by very few (1 to 5) individuals. Downstream samples before removal (stage 0) averaged 26.3 rare (= those representing less than 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 after complete removal. There is no evidence that any species were completely eliminated by the removal event; species that comprised at least 1% of all individuals counted in pre-removal downstream samples were always found after removal.

There was a significant Site×Stage interaction for the average Siltation index (Table 2). The average siltation index at the upstream site was lower during stage 1 than stage 0 or stage 2, whereas there were no significant differences among stages for either downstream site (Table 2, Figure 4). The lower siltation index at site 1 during stage 1 is the result of a downward trend that was evident prior to removal at all sites. The trend was interrupted at the downstream sites by a jump at the first sample date (approx 3 weeks) after the initial removal (Figure 4). 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, Figure 4).

There were strong temporal patterns in the diatom ordination but no separation of upstream and downstream sites at any stage (Figure 5). The first (horizontal) axis reflects a strong seasonal pattern in the relative abundances of diatom species. Seasonal differences mainly reflect 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, Navicula lanceolata in spring). Samples collected in 2001 tend to separate from 2000 samples along the second axis, with lower scores in 2001. Epiphytic species (e.g. Cocconeis placentula and C. pediculus) were strongly positively correlated with this axis, whereas motile species (especially Nitzschia and Navicula species) were negatively correlated.

#### Substrate and hydraulic characteristics

Mean particle size (Figure 6) decreased significantly at all sites after complete removal, but the average decrease was significantly greater at downstream than upstream sites (Table 3). The changes in mean particle size mainly reflect increases in the proportion of sand, which increased from 1.25 to 14.5% at downstream sites and from 2.75 to 10.0 % at upstream sites ( $P_{\text{Location} \times \text{Stage}} = 0.030$  for % sand, indicating a significantly greater increase at downstream sites).

Hydraulic characteristics within sampled areas did not vary among stages (Table 3). Upstream riffles (mean depth  $\pm$  SE =  $8.42 \pm 0.20$  cm) were slightly deeper than downstream riffles (mean  $\pm$  SE =  $7.60 \pm 0.27$  cm) throughout the study, but mean velocities were similar among all sites (mean  $\pm$  SE =  $0.43 \pm 0.01$  m s<sup>-1</sup> for both upstream and downstream sites).

## Discussion

A key assumption behind the growing call to restore rivers via dam removal is that the ecological benefits of removing dams will outweigh any ecological costs associated with the removal process. This assumption cannot be fully evaluated without proper understanding of how dam removals affect all components of the ecosystem, including biota that may not be specific targets of restoration, both upstream and downstream of the dam. Because of the potential for accumulated sediments to be transported downstream following dam removal, the risks of negative or unwanted ecological effects are perhaps greatest downstream of the dam, and among benthic biota in particular. Despite this, the responses of downstream benthic assemblages to dam removal have rarely been investigated. Our study was designed to quantify the magnitude and duration of responses by benthic algae and macroinvertebrates to the removal of a small dam. We documented significant reductions in macroinvertebrate abundance (~50 %) and diatom richness (~20 %) at downstream sites for at least twelve months after dam removal, but observed few changes in these attributes at upstream control sites. Algal biomass was also severely reduced (70%) at downstream sites in the year following dam removal, although less severe reductions (45%) also occurred upstream of the dam. The removal had no detectable effects on the composition or relative abundances of taxa within macroinvertebrate or diatom assemblages, and, therefore, no effects on several important metrics of community structure.

The reductions in macroinvertebrate abundance, diatom richness and algal biomass coincided with, and were likely related to, the downstream transport of predominantly sand and gravel sediments previously stored within the impoundment. Impoundment sediments were carried downstream by high flow events in the months following complete removal (Egan 2001), causing a substantial reduction in mean particle size that persisted throughout 2001 (Figure 6, see also Egan 2001). Fine sediments generally have negative impacts on benthic communities (Waters 1995, Wood and Armitage 1997), and sediments deliberately or accidentally released from reservoirs have previously been found to cause pronounced reductions in benthic densities, and sometimes diversity (Gray and Ward 1982, Marchant 1989, Doeg and Koehn 1994). It is possible that some of the observed impacts on downstream benthic assemblages in Manatawny Creek were caused directly by flooding (e.g. Lake 2000, Thomson 2002) rather than by the resultant sedimentation or other dam removal effects. Flooding occurred at all sites,

however, whereas prolonged reductions in invertebrate abundance and diatom diversity were only detected at downstream sites. While initial differences between upstream and downstream communities (e.g. proportionately more chironomids at downstream sites) might explain some differences in initial flood impacts, they are unlikely to explain the unusually slow recovery of downstream assemblages (e.g. see Thomson 2002 for rapid recovery of chironomids after floods). Thus, while it is impossible to separate completely the effects of floods and dam removal, there is strong evidence that their interaction had a greater impact on benthic communities than flooding alone.

The two-stage removal process made it easier to distinguish among alternative explanations for the observed biotic responses to the dam removal. For example, 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 significant biological changes during this stage, suggesting that potential changes in water quality following the impoundment's elimination were not a major factor affecting benthic organisms. This 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. The only apparent biotic impact of the initial removal was a significant increase in the Siltation Index (i.e., proportion of motile diatom taxa) at downstream sites relative to upstream sites, suggesting some downstream disturbance associated with the initial excavation process.

Benthic communities often recover rapidly from sedimentation impacts after sediment loads return to pre-disturbance levels (Gray and Ward 1982, Marchant 1989, Doeg and Koehn, 1994, Wood and Armitage 1997). Thus, the apparent downstream effects of released sediments are unlikely to be permanent in Manatawny Creek, because sediment from the former impoundment is continuing to move downstream and the bed is expected to become more like its pre-removal configuration over time (Egan 2001). Biological sampling in these downstream habitats in the fall of 2003, however, suggests that sediment transport and deposition is continuing to have adverse effects on fish assemblages (Horwitz, pers. comm.). Thus, complete biological recovery from increased sediment loads following small dam

removal could potentially take several-to-many years. This observation underscores the need for additional studies that quantify ecological responses to dam removal over longer time spans.

Given that the negative downstream impacts of removing the Manatawny dam will probably be temporary, an important question is whether removal will have any positive downstream impacts in the longer term. Prior to dam removal, downstream sites were sometimes characterized by nuisance algal growth ( $> 200 \text{ mg m}^{-2} \text{ chl-a}$ ) and consistently had poorer HBI scores, lower macroinvertebrate diversity (especially in EPT taxa) and proportionately more chironomids than upstream sites. Although algal biomass was lower after dam removal, there was no evidence of improvement in macroinvertebrate metrics up to a year after removal. The lower reaches of Manatawny Creek pass through a heavily urbanized catchment and have considerably more storm water inputs and less riparian vegetation than upstream reaches. These differences likely explain the depauperate macroinvertebrate assemblages and higher algal biomass at downstream sites relative to upstream sites prior to dam removal. Given that the Manatawny dam had minimal downstream effects on water quality (Bushaw-Newton et al. 2002), and that the urban impacts remain unabated, it seems unlikely that the dam removal per se will cause a substantial improvement in downstream ecological integrity. The reduction in algal biomass most likely reflects the combined impacts of flow disturbances (stochastic events unaffected by the removal of the small dam) and sedimentation (most likely a temporary impact of dam removal), and may not be indicative of any longer term impact of dam removal on primary production.

The moderate impact of the Manatawny Creek dam removal on downstream benthic communities appears to similar to that observed by Stanley et al. (2002) for dam removals in a Wisconsin stream (i.e. no effect on macroinvertebrate assemblage structure or condition metrics). Together with observations that even severely depleted benthic assemblages often recover rapidly once sediments accidentally or deliberately released from reservoirs are flushed from the system (Gray and Ward 1982, Doeg and Koehn 1994, Stanley and Doyle 2003), these results suggest that small dam removals may not have long-term deleterious impacts on downstream benthic communities. This in turn supports the notion that small dam removals will often have a net ecological benefit, as the benefits associated with restoring natural morphology and connectivity to rivers will often outweigh the short-term ecological impacts of downstream sedimentation following removal. For example, conversion of impoundments to free-

flowing reaches following dam removal often results in improved ecological integrity due to rapid shifts in the composition of both benthic macroinvertebrate and fish assemblages (Bushaw-Newton et al. 2002, Stanley et al. 2002). Conversely, small dams that have small impoundment areas and few downstream impacts may contribute little to total ecological impairment relative to other anthropogenic factors, especially in highly urbanized or agricultural systems. Thus, the removal of such dams may not be a restoration priority unless there are other major ways in which the dams are impacting ecological conditions (e.g. prevention of fish passage by migratory or resident species, poor water quality or other habitat problems). Alternatively, decisions to remove these dams may be influenced more strongly by safety and liability concerns than by a desire to improve environmental quality (e.g., Bednarek 2002).

As Stanley and Doyle (2003) suggest, dam removals may be best considered as ecological disturbances. The challenge for ecologists and managers is to predict the spatial and temporal scales of the physical disturbance and associated biological responses. Removal of small dams that have little effect on downstream water quality or flow regime might constitute pulse disturbances (Bender et al. 1984, Lake 2000) to downstream reaches: i.e., temporary increases in suspended and bed sediment loads that will cause short-term reductions in productivity and possibly diversity. Biotic communities can probably be expected to recover rapidly once sediments are flushed through the system. The magnitude of the biotic response, and the time to recover, will depend on both the magnitude and duration of the physical disturbance (determined by the volume and composition of stored sediment, and its decay mode and rate, Pizzuto 2002) and the characteristics of the organisms. Biota inhabiting streams that naturally experience frequent pulse disturbances may be highly resilient, having rapid life-cycles and /or mobile life-stages (Townsend and Hildrew 1994). Impacts may also be less pronounced if downstream assemblages are already impoverished and / or characterized by sediment-tolerant species, as may be the case in streams draining agricultural or urbanized catchments.

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## Figure Legends

**Figure 1.** Map showing the location of Manatawny Creek, the removed dam and the sampling sites.

5 **Figure 2.** Changes in a) total macroinvertebrate density, b) total taxa richness, c) Ephemeroptera, Plecoptera & Trichoptera taxa richness and d) Hilsenhoff's Biotic Index, at upstream (solid symbols) and downstream (open symbols) sites over the study period (location means  $\pm 1$  S.E., n=2 sites per location). Timing of initial and final removal events are indicated by vertical dashed lines, and the hydrograph is plotted on each graph to show timing of flood events. Hydrograph data were obtained from U.S.  
10 Geological Survey gauging station number 01471980 (Lat 40°16'22", long 75°40'49") located approximately 4.5 kilometers upstream from the dam and 5.0 km upstream from the river mouth.

**Figure 3.** Non-metric Multidimensional Scaling (NMDS) ordination of macroinvertebrate assemblages at sites upstream (solid symbols) and downstream (open symbols) of the dam throughout the study. Each  
15 stage is plotted on separate axis for clarity (a single ordination was performed). Symbol shape indicates sample date as indicated in legend. The NMDS was based on a Bray-Curtis similarity matrix derived from square root transformed counts of macroinvertebrate taxa aggregated by site and date.

**Figure 4.** Changes in a) chlorophyll-a concentrations, b) species richness, and c) diatom-based Siltation  
20 Index, at upstream (solid symbols) and downstream (open symbols) sites over the study period (location means  $\pm 1$  S.E., n=2 sites for downstream and 1 site for upstream). Timing of initial and final removal events are indicated by vertical dashed lines, and the hydrograph is plotted on each graph to show timing of flood events.

25 **Figure 5.** Non-metric Multidimensional Scaling (NMDS) ordination of diatom assemblages at sites upstream (solid symbols) and downstream (open symbols) of the dam throughout the study. Each stage is plotted on separate axis for clarity (a single ordination was performed). Symbol shape indicates sample date as indicated in legend. The NMDS was based on a Bray-Curtis similarity matrix derived from square root transformed counts of diatom species.

30

**Figure 6.** Changes in mean particle size ( $\phi$ ) upstream (solid circles) and downstream (open circles) of the impoundment over the study period.  $\phi$  values are location means  $\pm 1$  S.E. with n=2 sites per location. Timing of initial and final removal events are indicated by vertical dashed lines, and the hydrograph is plotted on each graph to show timing of flood events.



Table 1. ANOVA results for macroinvertebrate metrics. The denominator mean square terms used in F-tests for each term are indicated by parenthesized numbers (corresponding to supertext term numbers) after each term, with no number indicating that term was tested against the residual error. Bold type *P* values are significant at  $\alpha=0.05$ . The final row summarizes the results of group mean comparisons examining the nature of significant Location, Stage or interaction effects.

	df	Total Density			Number of Taxa			Number EPT taxa			HBI		
		SS	<i>F</i>	<i>P</i>	SS	<i>F</i>	<i>P</i>	SS	<i>F</i>	<i>P</i>	SS	<i>F</i>	<i>P</i>
<sup>1</sup> Location (6)	1	0.001	0.001	0.982	495.772	18.916	<b>0.002</b> <sup>§</sup>	165.525	19.400	<b>0.002</b> <sup>§</sup>	11.789	38.976	<b>&lt;0.001</b> <sup>§</sup>
<sup>2</sup> Stage (5)	2	20.498	2.940	0.110	830.653	2.160	0.178	234.854	1.279	0.330	8.752	1.489	0.282
<sup>3</sup> Location × Stage (6)	2	12.605	6.056	<b>0.025</b> *	42.721	0.815	0.476	14.590	0.855	0.461	0.497	0.822	0.474
<sup>4</sup> Site(L) (8)	2	1.9349	2.372	0.125	42.985	1.823	0.194	4.533	0.663	0.529	0.886	11.781	<b>&lt;0.001</b>
<sup>5</sup> Date(Stage)	8	27.887	14.061	<b>&lt;0.001</b>	1538.280	31.499	<b>&lt;0.001</b>	734.678	32.628	<b>&lt;0.001</b>	23.509	78.186	<b>&lt;0.001</b>
<sup>6</sup> Location × Date(S)	8	8.325	4.198	<b>&lt;0.001</b>	209.675	4.293	<b>&lt;0.001</b> <sup>£</sup>	68.259	3.032	<b>0.003</b> <sup>£</sup>	2.420	8.048	<b>&lt;0.001</b> <sup>¥</sup>
<sup>7</sup> Stage × Site(L) (8)	4	2.005	1.229	0.338	58.696	1.244	0.332	15.048	1.101	0.390	1.159	2.815	0.061
<sup>8</sup> Site(L) × Date(S)	16	6.526	1.645	0.062	188.665	1.932	<b>0.020</b>	54.656	1.214	0.261	1647	2.739	<b>0.001</b>
<sup>9</sup> Residual	176	43.384			1074.384			495.364			6.615		
Differences among means		*Upstream: Stage 0 = Stage 1 = Stage 2 *Downstream: Stage 0 = Stage 1 < Stage 2			§Upstream > Downstream £except at 31-5-00 (stage 0), 1-9-00, 20-10-00 (stage 1) and 28-9-01 (stage 2).			§Upstream > Downstream £except at 31-5-00 (stage 0) and 1-9-00 (stage 1).			§Upstream > Downstream ¥size of difference temporally variable		

Table 2 ANOVA results for algal metrics. Table format is the same as Table 1

	df	No. Taxa			Chlorophyll a			Siltation Index		
		SS	<i>F</i>	<i>P</i>	SS	<i>F</i>	<i>P</i>	SS	<i>F</i>	<i>P</i>
<sup>1</sup> Site	2	0.039	1.627	0.224	0.591	1.446	0.267	0.008	0.258	0.775
<sup>2</sup> Stage (4)	2	0.149	2.698	0.121	12.768	4.951	<b>0.035</b>	0.103	0.597	0.571
<sup>3</sup> Site × Stage	4	0.159	3.323	<b>0.033*</b>	2.915	3.565	<b>0.027<sup>§</sup></b>	0.225	3.667	<b>0.024<sup>¥</sup></b>
Site <sub>down</sub> × Stage	2	0.050	2.070	0.155	0.906	2.220	0.137	0.048	1.595	0.230
Site <sub>down v up</sub> × Stage	2	0.109	4.542	<b>0.025*</b>	2.009	4.923	<b>0.020<sup>§</sup></b>	0.177	5.913	<b>0.011<sup>¥</sup></b>
<sup>4</sup> Date (Stage) <sup>a</sup>	9	0.249	2.325	0.061	11.604	6.308	<b>&lt;0.001</b>	0.776	5.624	<b>0.001</b>
<sup>5</sup> Residual <sup>a</sup>	18	0.215			3.679			0.276		
Differences among means		*Downstream: Stage 0 = Stage 1 > Stage 2 *Upstream: Stage 0 = Stage 1 = Stage 2			<sup>§</sup> Downstream: Stage 0 = Stage 1 >> Stage 2 <sup>§</sup> Upstream: Stage 0 = Stage 1 > Stage 2			<sup>¥</sup> Downstream: Stage 0 = Stage 1 = Stage 2 <sup>¥</sup> Upstream: Stage 0 > Stage 1 < Stage 2		

<sup>a</sup> Residual error includes error from untestable Site × Date(S) term, F-test for term 4 assumes this component is zero.

Table 3. ANOVA results for habitat variables. Table format is the same as Table 1.

	df	Mean Phi			Mean Velocity			Mean Depth		
		SS	<i>F</i>	<i>P</i>	SS	<i>F</i>	<i>P</i>	SS	<i>F</i>	<i>P</i>
<sup>1</sup> Location (6)	1	1.113	1.251	0.296	0.000	0.000	0.999	35.415	6.864	<b>0.031</b> <sup>§</sup>
<sup>2</sup> Stage (5)	2	72.706	30.591	<b>&lt;0.001</b>	3.492	2.698	0.127	160.947	1.229	0.343
<sup>3</sup> Location × Stage (6)	2	8.744	4.915	<b>0.041</b> *	0.022	1.059	0.391	5.138	0.498	0.625
<sup>4</sup> Site(L) (8)	2	5.046	8.419	<b>0.003</b>	0.003	0.139	0.871	110.975	14.629	<b>&lt;0.001</b>
<sup>5</sup> Date(Stage) (9)	8	9.507	1.188	<b>&lt;0.001</b>	5.177	5.325	<b>&lt;0.001</b>	524.024	24.567	<b>&lt;0.001</b>
<sup>6</sup> Location × Date(S)	8	7.117	0.890	<b>0.006</b>	0.081	0.084	0.999	41.279	1.935	0.057
<sup>7</sup> Stage × Site(L) (8)	4	3.437	2.867	0.058	0.024	0.547	0.704	13.016	0.858	0.510
<sup>8</sup> Site(L) × Date(S)(9)	16	4.795	0.300	0.515	0.178	0.091	0.999	60.688	1.423	0.136
<sup>9</sup> Error	176	55.278			21.386			469.272		
Differences among means		*Downstream: Stage 0 = Stage 1 << Stage 2  *Upstream: Stage 0 = Stage 1 < Stage 2						§Upstream > Downstream		

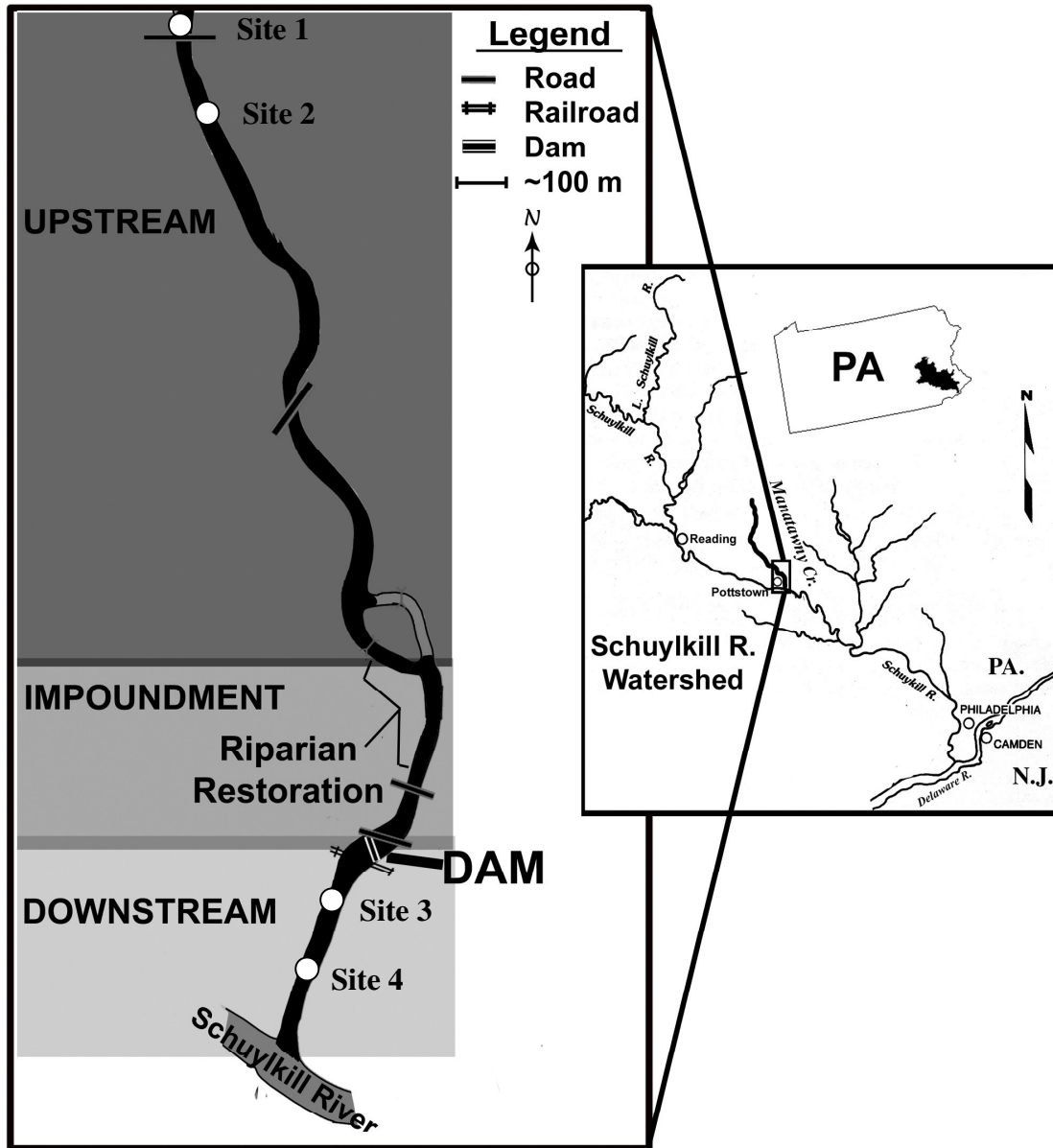
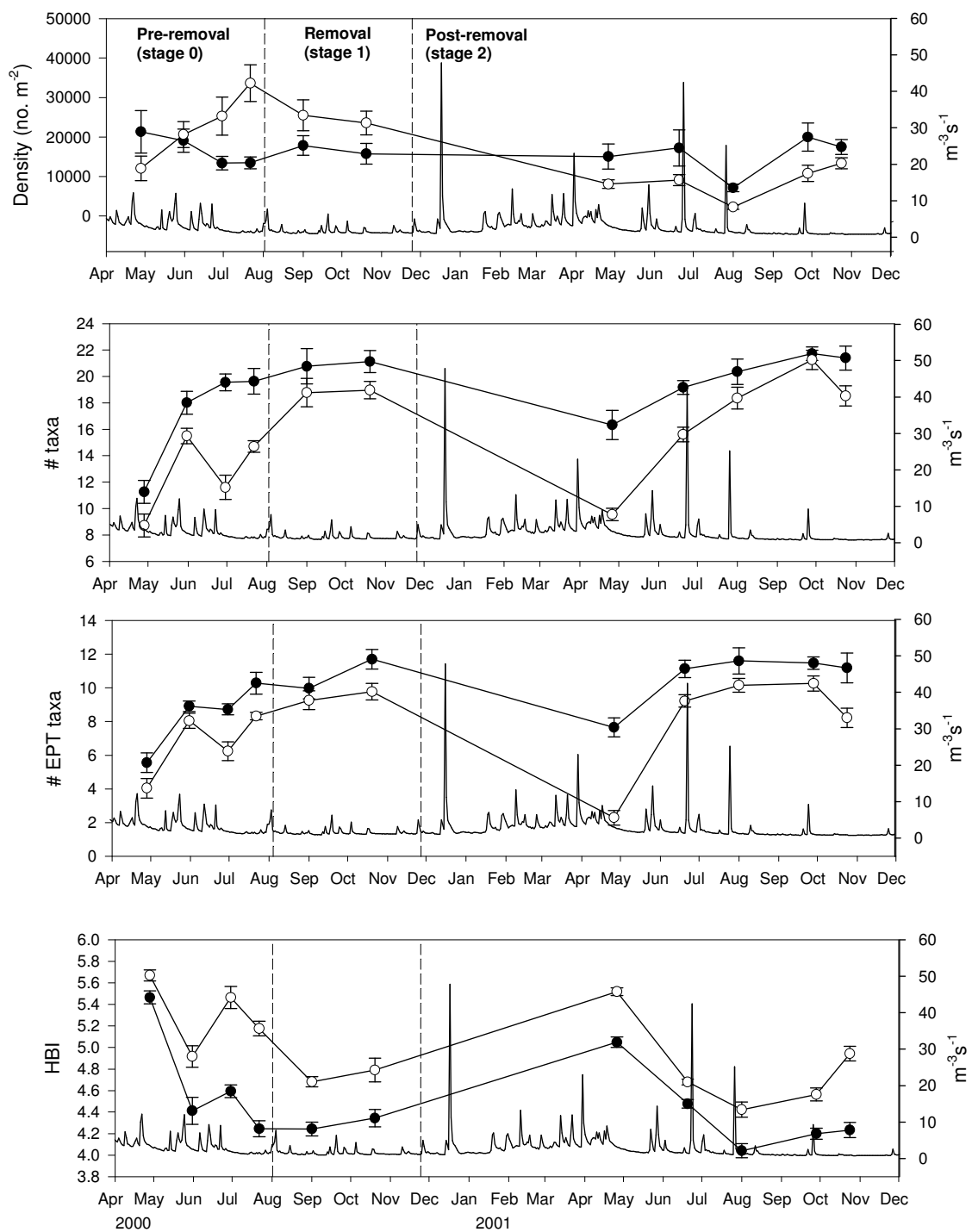
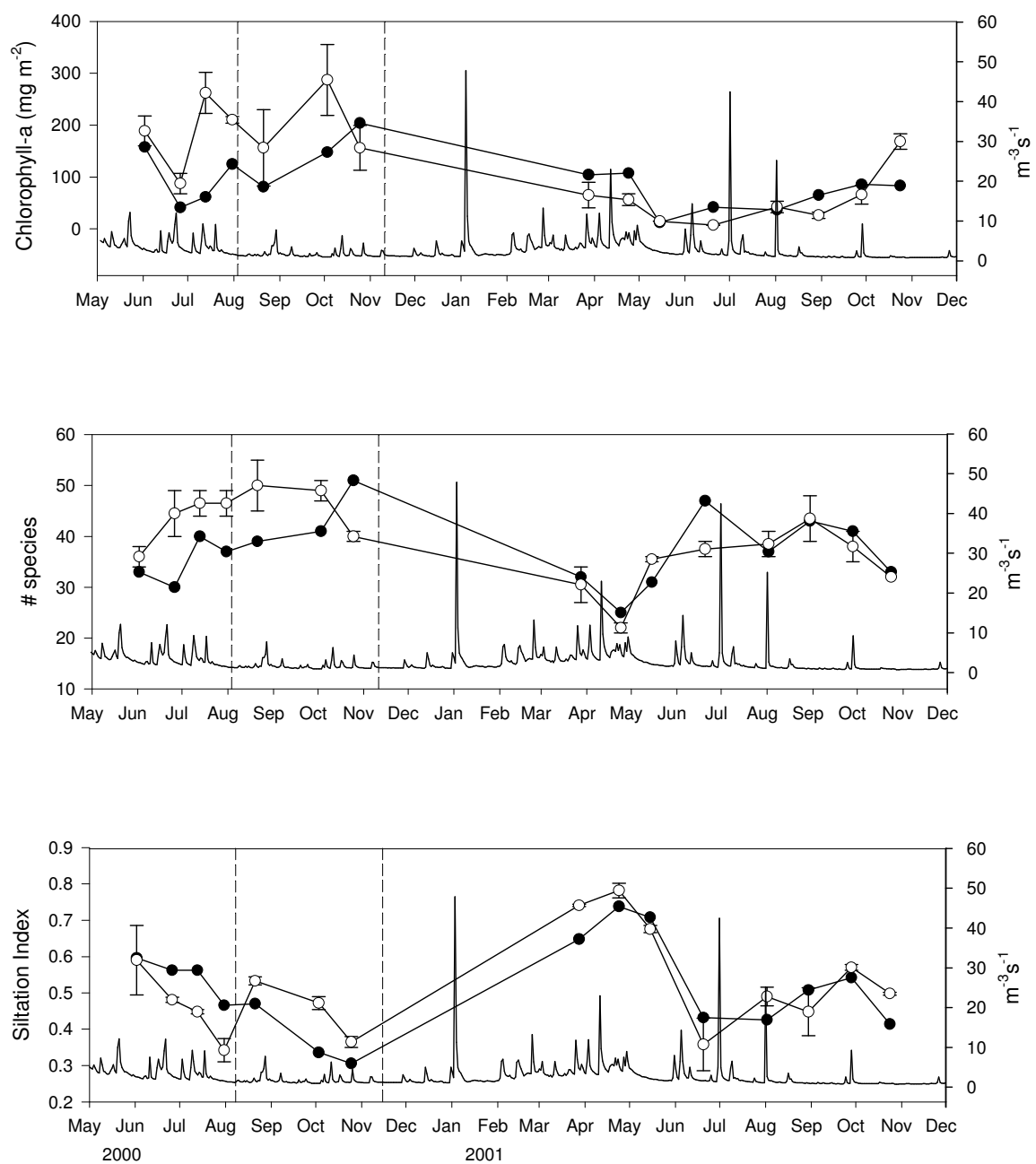


Figure 1

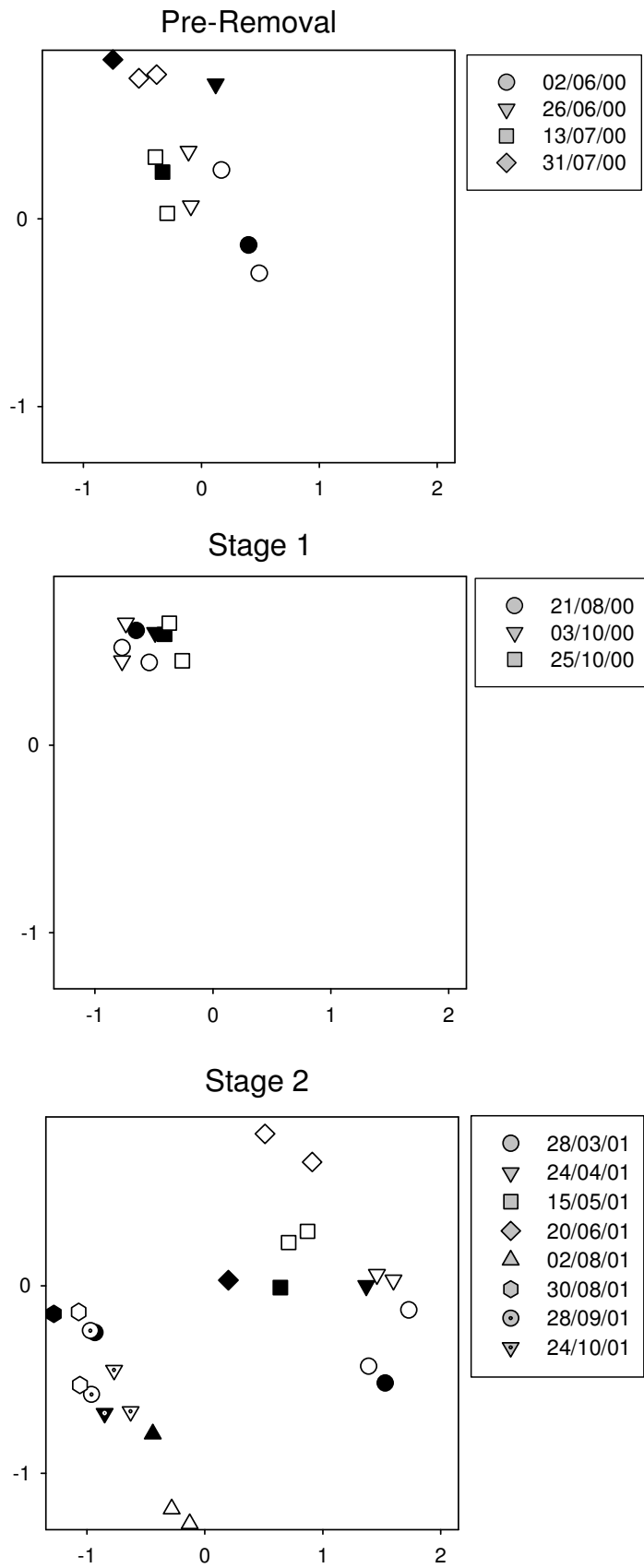


**Figure 2**

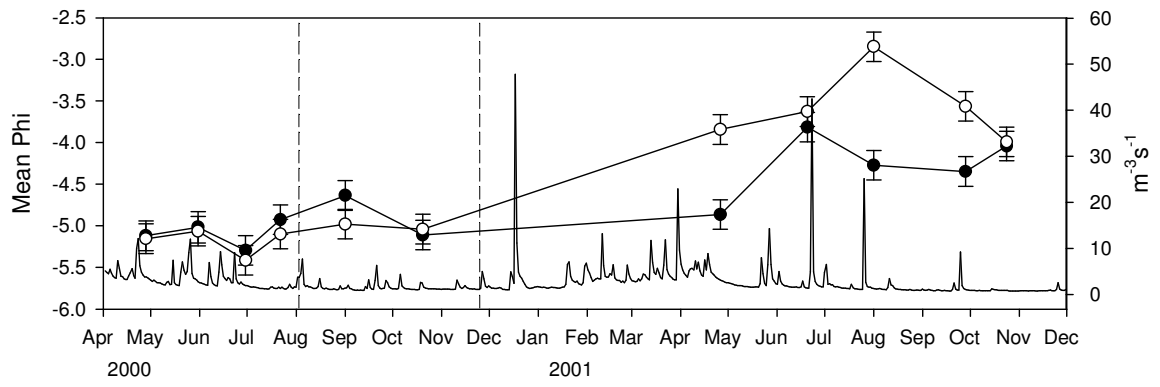




**Figure 4**



**Figure 5**



**Figure 6**